

New records and new species of springtails (Collembola: Entomobryidae, Paronellidae) from lava tubes of the Galápagos Islands (Ecuador)

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Abstract

The Collembola fauna of the Galápagos Islands is relatively unexplored with only thirty-five reported species. Entomobryoidea, the most diverse superfamily of Collembola, is underrepresented, with only five species reported from the Galápagos. Here we present the findings of the first survey of Collembola from Galápagos lava tube caves, providing a significant update to the total number of entomobryoid Collembola species reported from the Galápagos Islands. Collections made during a March 2014 expedition to study lava tubes of the islands yielded new records for seven species of Entomobryoidea, including four genera not previously reported from the Galápagos Islands: *Coecobrya*, *Entomobrya*, *Heteromurus*, and *Salina*. As a result, three new species (*Entomobrya darwini* Katz, Soto-Adames & Taylor, **sp. n.**, *Pseudosinella vulcana* Katz, Soto-Adames & Taylor, **sp. n.**, and *Pseudosinella stewartpecki* Katz, Soto-Adames & Taylor, **sp. n.**) are described and new diagnoses are provided for *Heteromurus* (*Heteromurtrella*) *nitens* Yosii, 1964, *Lepidocyrtus nigrosetosus* Folsom, 1927 and *Pseudosinella intermixta* (Folsom, 1924). *Lepidocyrtus leleupi* Jacquemart, 1976 is synonymized with *L. nigrosetosus*. An updated checklist of all species within the superfamily Entomobryoidea reported from the Galápagos Islands is provided.

Keywords

Cave, chaetotaxy, Entomobryomorpha, Entomobryoidea, species checklist, synonymy, taxonomy

Introduction

Like the Hawaiian and Canary islands, major islands of the Galápagos archipelago are comprised of shield volcanoes (Fig. 1A). The Galápagos volcanoes are on the Nazca oceanic plate over the Galápagos hotspot, far from plate boundaries (Holden and Dietz 1972, Hey 1977, Toulkeridis 2011). The main Galápagos Islands are located east of the N-S-trending East Pacific Rise and south of the E-W-trending Galápagos Spreading Center and some 1000 km west of the Ecuadorian mainland. Associated with the shield volcanoes are hundreds of relatively small, cinder cones, ash cones, and spatter cones. These islands range in age from 0.0032 to 4 million years, with still active volcanoes on the younger islands (White et al. 1993, Geist et al. 2014, Global Volcanism Program 2015), with even older islands now represented only by seamounts. These geodynamics and the ever-changing volcanic development of the Galápagos Islands has given rise to conditions under which the unique endemic life on these islands has evolved (Darwin 1859). Evidence now suggests that for at least some animal taxa, colonization of the Galápagos archipelago likely took place before many of the present islands had emerged from the ocean (Christie et al. 1992, Torres-Carvajal et al. 2014, Husemann et al. 2015).

The composition of the fauna of the Galápagos Islands is shaped by the volcanic history of the islands, as well as the remoteness of the archipelago from the mainland. This is even more true for the subterranean fauna, comprised of “wrecks of ancient life” (Darwin 1859), living in the relatively stable, cool, humid conditions (Ashmole et al. 1992) of lava tubes on the slopes of the various shield volcanoes that form these islands. These lava tube caves (e.g., Fig. 1B) form from heated basalt flowing down the slopes of volcanoes, forming preferential flow paths that eventually drain, creating the caves. Various smaller cracks and other subterranean voids occur both in the relatively smooth pāhoehoe lava flows and in the more rugged ‘a‘ā lava (Harris and Rowland 2015), providing innumerable places in which invertebrates may live (Howarth 1991, Peck 2001, Stone et al. 2004, Howarth et al. 2007, Toulkeridis 2011).

Diversity and relationships among subterranean animals, shaped by vicariance and dispersal are a common theme for island lava tube faunas of Hawaii (Howarth 1991, Juan et al. 2010), the Canary Islands (Oromí et al. 1991, Juan et al. 2000, Naranjo Morales and Abreu 2015), Rapa Nui (Easter Island) (Wynne et al. 2014), and the Galápagos Islands (Peck 1990). However, the inaccessibility of much of the Galápagos archipelago, due to a lack of roads and extremely rugged terrain, have restricted biological inventories of subterranean ecosystems in comparison to the Hawaiian (more than 50 terrestrial troglobites, Howarth 1991) and Canary archipelagos (more than 160 species of invertebrates unique to the underground environment, Naranjo Morales and Abreu 2015). Most recent work on Galápagos has been carried out, or summarized, by Stewart B. Peck (Peck and Kukalova-Peck 1986, Peck and Shear 1987a, 1987b, Peck

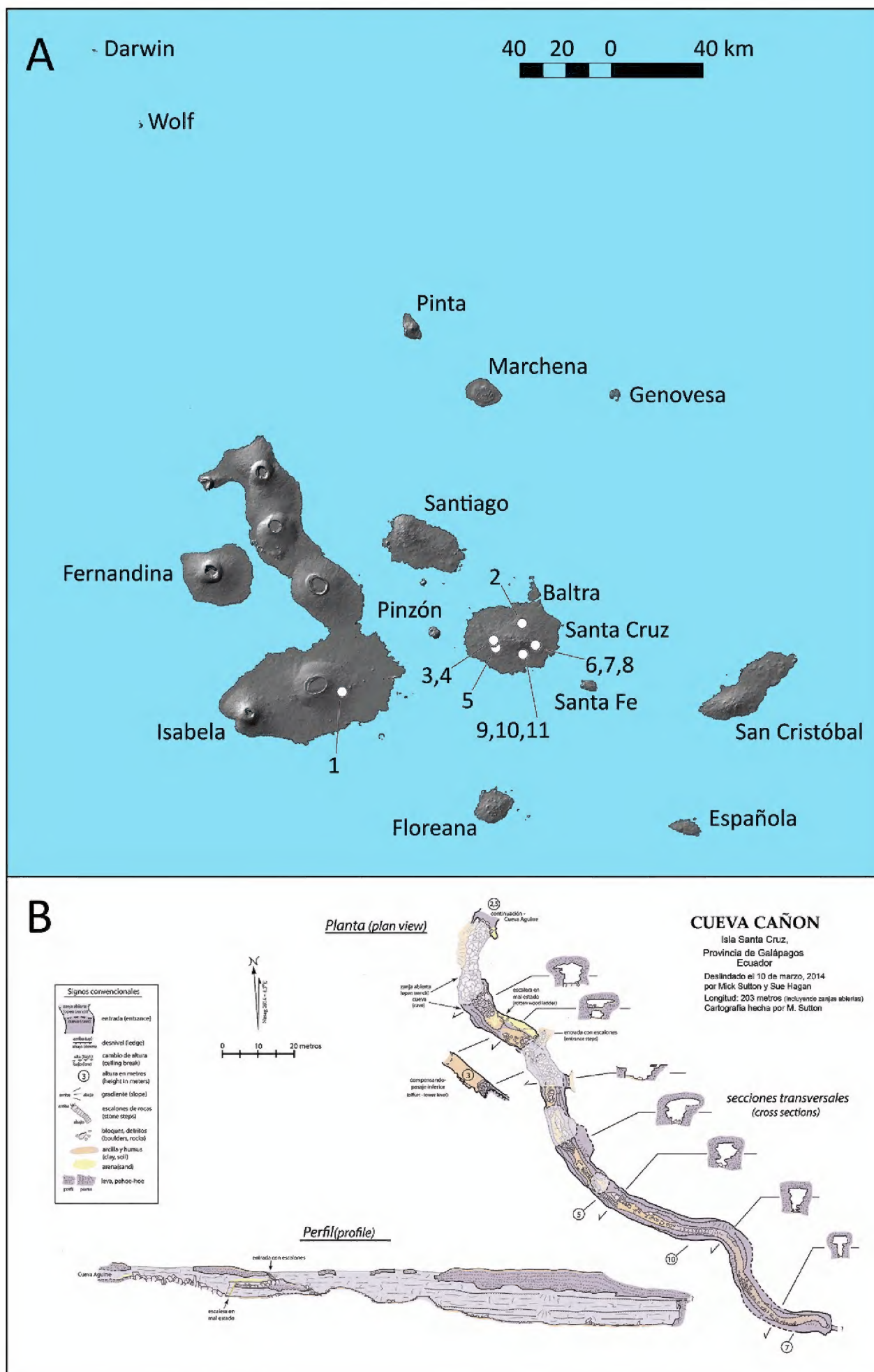


Figure 1. A Galápagos Islands, Ecuador, with major islands labeled and locations of caves sampled indicated by numbered circles: **1** La Cueva de Sucre **2** La Llegada **3** Cueva Chato **2** **4** Cueva Chato **1** **5** Cueva Primicias **6** Cueva Cañón, **7** Cueva Aguirre **8** Cueva Cascajo, **9** Cueva Soyla **10** Cueva JoAnn, and **11** Cueva Gallardo **B** Map of Cueva Cañón (Santa Cruz Island, Galápagos Islands, Ecuador), which is typical of the morphologies of the lava tube caves sampled. Maps of many of the other caves sampled during this study are available in Addison (2011) and Toulkeridis and Addison (2015).

1990, 2001, Peck and Finston 1993) who reports more than 55 eyeless and reduced eye arthropods, many of these from caves or cave entrances (Peck 1990, 2001).

Earlier analyses by Peck (1990) and Taylor et al. (2012) suggested that much remains to be learned regarding the subterranean fauna of the Galápagos Islands. These analyses helped build the justification for a multidisciplinary expedition, including the biological collections reported here, studying lava tube caves in the Galápagos Islands in March 2014. This expedition was conducted in association with the 16th International Symposium of Vulcanospeleology (Puerto Ayarro, Santa Cruz, Galápagos Islands, Ecuador) (Toulkeridis and Addison 2015), and built upon earlier field studies led by two of the authors (TT, AA). Here we make a contribution regarding the entomobryoid springtails (Collembola) of the Galápagos Islands as part of the ongoing studies of lava tube caves of the islands by our research team.

Thirty-five species of Collembola have been reported from the Galápagos Islands (Peck 2001); 18 in the order Poduromorpha (Stach 1932, Gama 1986, Najt et al. 1991) and 17 in the order Entomobryomorpha, 12 of which are in the family Isotomidae (Thibaud et al. 1994). The superfamily Entomobryoidea is underrepresented, with only 5 species formally reported from the Galápagos (Folsom 1924, Jacquemart 1976). The ostensible lack of diversity is most certainly due to the limited number of collections where specimens were subsequently identified and published. All 35 reported species were identified and described in six publications from material obtained from just four collections: the Williams Galápagos Expedition 1923–1925 (Folsom 1924); the Norwegian Zoological Expedition to the Galápagos Islands 1925, conducted by Alf Wollebæk (Stach 1932); the Belgian Zoological Mission to the Galápagos Islands and Ecuador led by N. and J. Leleup, 1964–1965 (Jacquemart 1976, Gama 1986, Najt et al. 1991, Thibaud et al. 1994); and collections made by Guy Coppois 1974–1976 (Najt et al. 1991, Thibaud et al. 1994).

Entomobryoidea is the most diverse superfamily of Collembola, representing more than one fourth of all described species worldwide (Bellinger et al. 2015). Species in the genera *Pseudosinella*, *Sinella*, *Coecobrya*, and *Trogolaphysa*, represent a large proportion of the springtail diversity found in New World caves, but the springtail fauna of Galápagos lava tubes has not been documented and these genera (except *Pseudosinella*) have not been reported from the islands. The purpose of this study is to describe and document all species in the superfamily Entomobryoidea collected during the recent 2014 bioinventories of Galápagos lava tubes. Here we provide descriptions for three new species endemic to the Galápagos, three new diagnoses, and new records for four genera and seven species. We also include an updated checklist of all species in the superfamily Entomobryoidea reported from the Galápagos Islands.

Methods

Geologic setting on Santa Cruz and Isabela islands. The Santa Cruz shield volcano is subdivided into two main units (Bow 1979), an older Platform Unit with an age of 1.3–1.1 Ma and a younger unit represented by lavas of the Shield Series with ages as

young as 30–20 ka (Bow 1979, White et al. 1993, Geist et al. 2014). Sierra Negra on Isabela Island is a young, volcanically active shield volcano with various eruptive centers and lava fields that have been divided into five distinctive age groups, all being younger than 6000 years (Reynolds et al. 1995). Ten eruptions have occurred on Sierra Negra in the last 200 years, with the most recent eruption in October 2005 (Geist et al. 2008).

Specimen collection and preparation. Collections for this study were made at lava tube caves on Santa Cruz and Isabela islands, Galápagos (Fig. 1A) from 8 through 21 March 2014. Bioinventories were conducted in eleven lava tube caves (Table 1): ten on Santa Cruz Island and one on the Sierra Negra volcano on Isabela Island (Galápagos Islands, Ecuador). Caves were selected on the basis of opportunity, distribution across Santa Cruz Island, and coordination with other ongoing research (mapping, geology, soil science). For caves on Santa Cruz Island, handheld meters were used at most sites to collect temperature, humidity and light data in surface, entrance, twilight and dark zone habitats. Individual specimens were collected by hand from ceiling, walls, and floor in terrestrial or drip pool (Fig. 2A) microhabitats throughout the lava tubes, using a paintbrush moistened in alcohol, or with an aspirator. Where accumulated leaf litter deposits were encountered, litter samples were collected into plastic bags and then extracted for 2–4 days using cloth Berlese funnels heated with 25 watt light bulbs. All material was preserved in 70% ethanol.

Individuals sampled were sorted under a dissecting microscope to morphospecies and photographed to record color pattern and body shape prior to slide mounting. All slide-mounted specimens were cleared with Nesbitt's solution and mounted with Hoyer's medium (Mari Mutt 1979) in preparation for light microscopy. Sex was determined by the observation of genital plate morphology. Specimens where genital plate morphology was obscured are listed in material examined sections without a sex determination. Illustrations were hand-drawn under a camera lucida, scanned, with final drawings created using Adobe Illustrator.

Table 1. List of lava tube caves in the Galápagos Islands (Ecuador) that were sampled for invertebrates in March 2014. Elevations based on 3m DEM data. Lengths and cave maps are from cited sources. Cueva Aguirre is not the same as Cueva de Raul Aguirre of Hernández et al. (1992).

Cave	Island	Elevation (m)	Surveyed Length (m)	References
La Cueva de Sucre	Isabela	379	340	Addison (2011), Toulkeridis and Addison (2015)
Cueva Aguirre	Santa Cruz	304	574	Present study
Cueva Cañón	Santa Cruz	304	203	Present study (Figs 1B, 2B)
Cueva Cascajo	Santa Cruz	275	3010	Hernández et al. (1992), Gulden (2015)
Cueva Chato 1	Santa Cruz	344	515	Toulkeridis and Addison (2015), Gulden (2015)
Cueva Chato 2	Santa Cruz	373	457	Toulkeridis and Addison (2015), Gulden (2015)
Cueva Gallardo	Santa Cruz	213	2316	Hernández et al. (1992), Toulkeridis and Addison (2015), Gulden (2015)
Cueva JoAnn	Santa Cruz	208	80	Toulkeridis and Addison (2015)
Cueva Primicias	Santa Cruz	265	640	Toulkeridis and Addison (2015)
Cueva Soyla	Santa Cruz	212	1038	Toulkeridis and Addison (2015), Gulden (2015)
La Llegada	Santa Cruz	251	2066	Toulkeridis and Addison (2015), Gulden (2015)

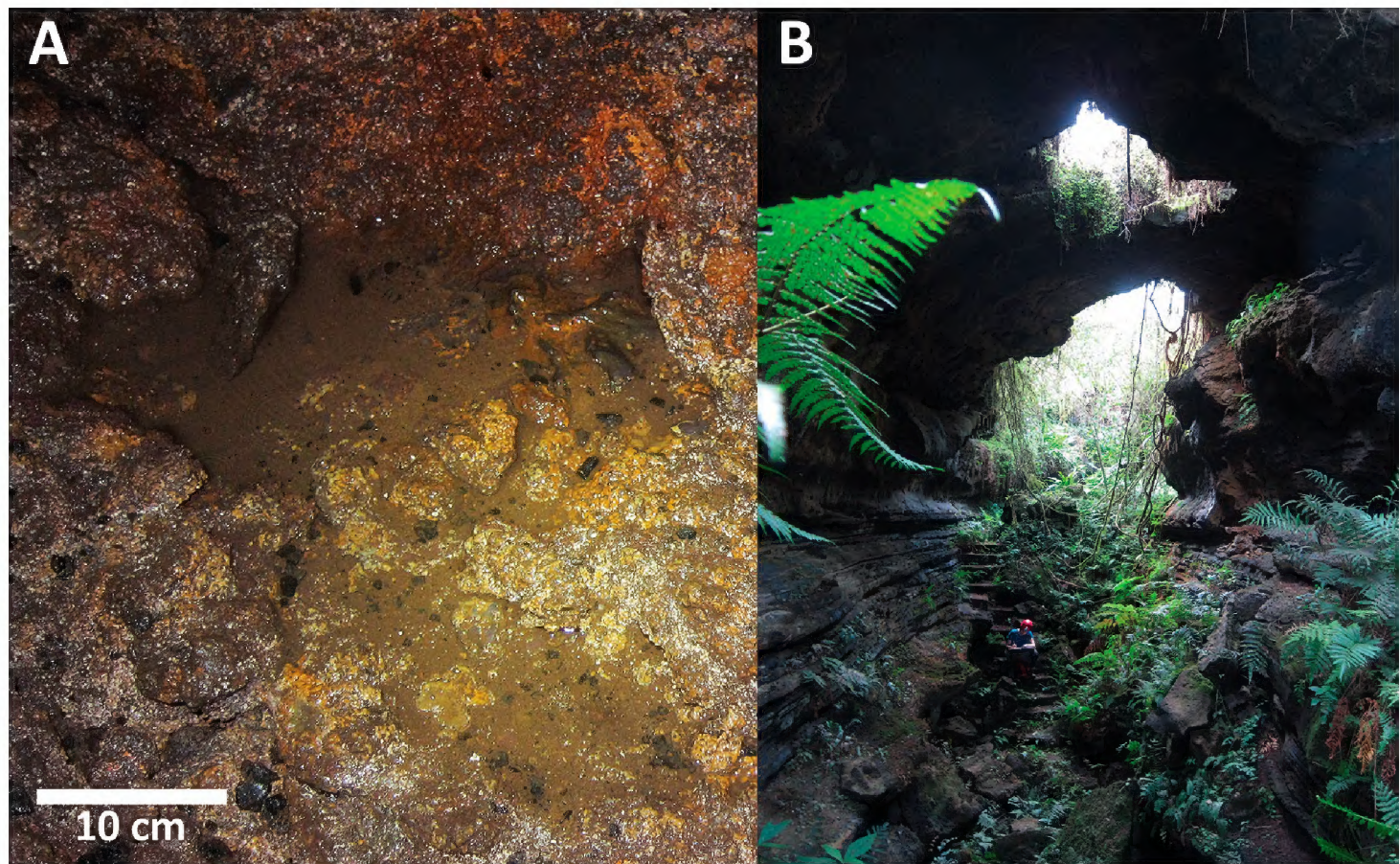


Figure 2. A Drip pool in dark zone of Cueva Chato 2 (Santa Cruz Island, Galápagos Islands, Ecuador), where *Pseudosinella vulcana* sp. n. was collected from surface film. Photo by SJT, 15 March 2014 **B** Entrance of Cueva Cañón (Santa Cruz Island, Galápagos Islands, Ecuador), where *Lepidocyrtus nigrosetosus* was collected. Photo by SJT, 10 March 2014.

Chaetotaxy nomenclature. Descriptions of dorsal body chaetotaxy follow the nomenclature established by Szeptycki (1979); the dorsal head chaetotaxy follows Jordana and Baquero (2005) and Soto-Adames (2008). Traditional dorsal chaetotaxy nomenclature for *Pseudosinella* established by Gisin (1967) is referred to in some descriptions for comparison and simplicity. See Soto-Adames (2010a) for comments and comparisons between nomenclature systems. All descriptions of labial chaetotaxy follow the nomenclature of Chen and Christiansen (1993).

Taxonomic classification. The suprageneric classification follows Soto-Adames et al. (2008).

Abbreviations and symbols. Abbreviations used in this paper are as follows: Ant. I–IV, antennal segments 1–4; Hd, head; Th. II, mesothorax; Th. III, metathorax; Abd. I–V, abdominal segments 1–5; Mc, macrosetae; mc, microsetae. See Figure 5F–J for symbol legend.

Deposition of types and material examined. Specimens examined are deposited in the following institutions: Illinois Natural History Survey Insect Collection, Illinois Natural History Survey, Prairie Research Institute, University of Illinois Urbana-Champaign, Urbana, Illinois, USA (INHS); Terrestrial Invertebrates Collection of the Charles Darwin Research Station, Puerto Ayora, Santa Cruz, Galápagos, Ecuador (CDRS); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS).

Results

Invertebrate samples were collected from all eleven caves from all caves zones. Specimens of Entomobryoidea were found from eight caves (Santa Cruz Island: Cueva Aguirre, Cueva Cañón, Cueva Cascajo, Cueva Chato 1, Cueva Chato 2, Cueva Gallardo, La Llegada; Isabella Island: La Cueva de Sucre). The lava tube caves varied from dry and largely barren of organic deposits to moist and containing organic deposits, soils, and water pools. The sites examined during this study are on the slopes of two shield volcanoes – Santa Cruz Island (elevation: 964 m) and Sierra Negra on Isabela Island (elevation: 1124 m). These caves are all in lava flows of sufficient age to have become largely covered with vegetation and to have significant settling and collapse resulting in various surface connections and tube segmentation (e.g., Figs 1B, 2B). Measured light levels ranged from 91,900 lux on the surface to 0 lux in the dark zone, air temperatures ranged from 37.3 °C in direct sunlight and 32.8 °C in the shade on the surface to 21.9 °C in the dark zone, soil temperatures ranged from 31.7 °C on the surface to 20.8 °C in the dark zone, and relative humidity ranged from 37.3% on the surface to 93.7% in dark zone, deep-cave habitats (Fig. 3). Most springtails were taken in Berlese leaf

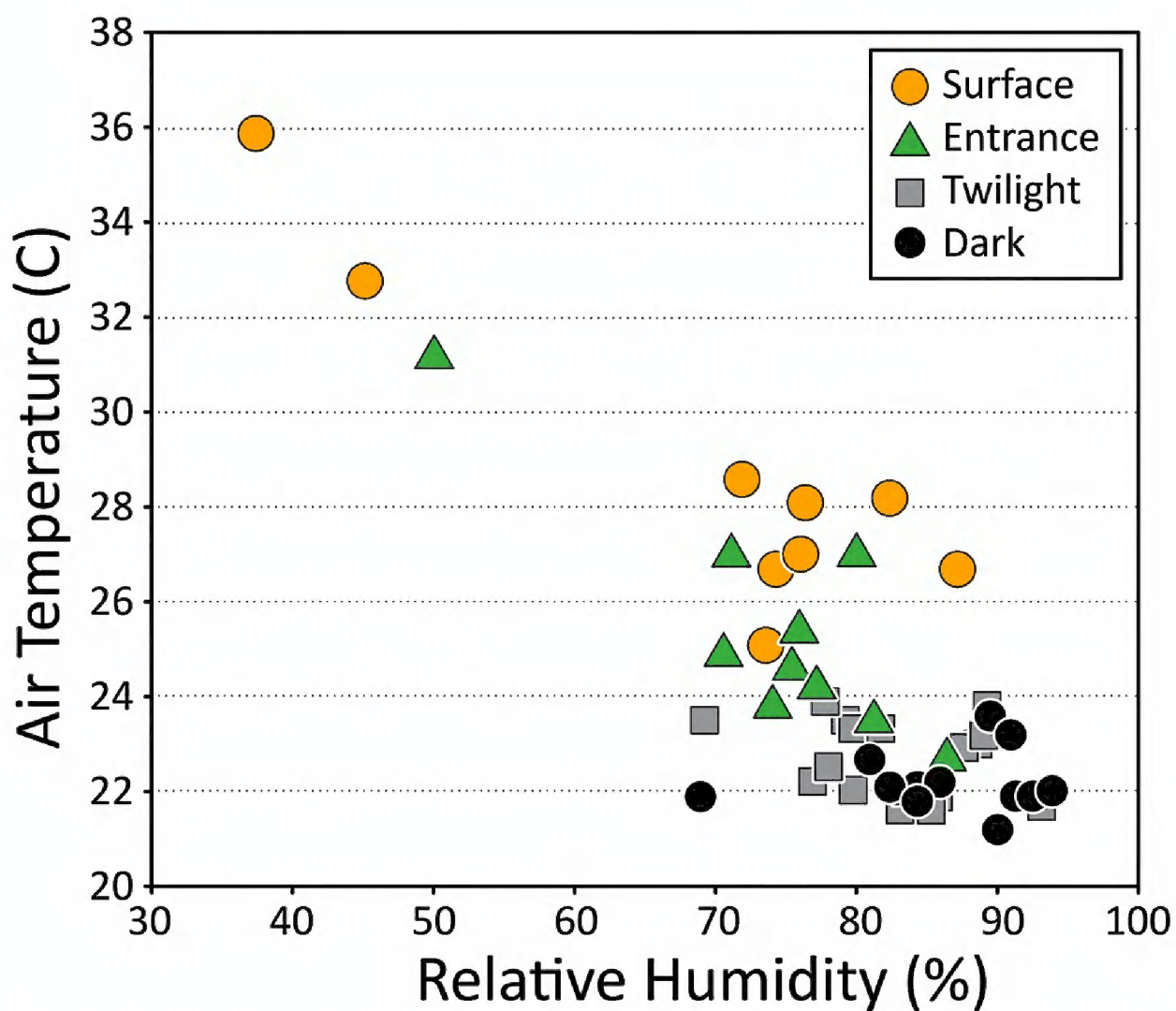


Figure 3. March 2015 relative humidity (%) and air temperature (°C) by cave zone for nine caves (Cueva Cañón, Cueva Cascajo, Cueva Chato 1, Cueva Chato 2, Cueva Gallardo, Cueva JoAnn, Cueva Primicias, Cueva Soyla, and La Llegada) on Santa Cruz Island, Galápagos Islands, Ecuador, where biological sampling took place during this study.



Figure 4. Entrance area of La Llegada (Santa Cruz Island, Galápagos Islands, Ecuador), where *Pseudosinella stewartpecki* sp. n. and *Cyphoderus* cf. *agnostus* were collected. Photo by SJT, 12 March 2014.

litter and moss samples in the entrance zone of caves (e.g., Figs 2B, 4), with specimens individually hand-collected in deep cave habitats, such as drip pools (Fig. 2A) or isolated woody debris.

Taxonomy

Family Entomobryidae

Heteromurus (*Heteromurtrella*) *nitens* Yosii, 1964

Figs 5–6

Descriptive notes. *Color.* Background color white (Fig. 5A), with orange granules scattered across head and body.

Head. Apical pin seta on Ant. IV present (Fig. 5B). Dorsal chaetotaxy of head as in Figure 5C: row An with 7 or 8 Mc; Mc A0, A2, A3, A4 present, A5 present as mc; row M with Mc M1 and M2 displaced anteriorly, forming cluster with series A, mc M0, M3 and M4 present, 2 additional mc present, including M3p, posterior to

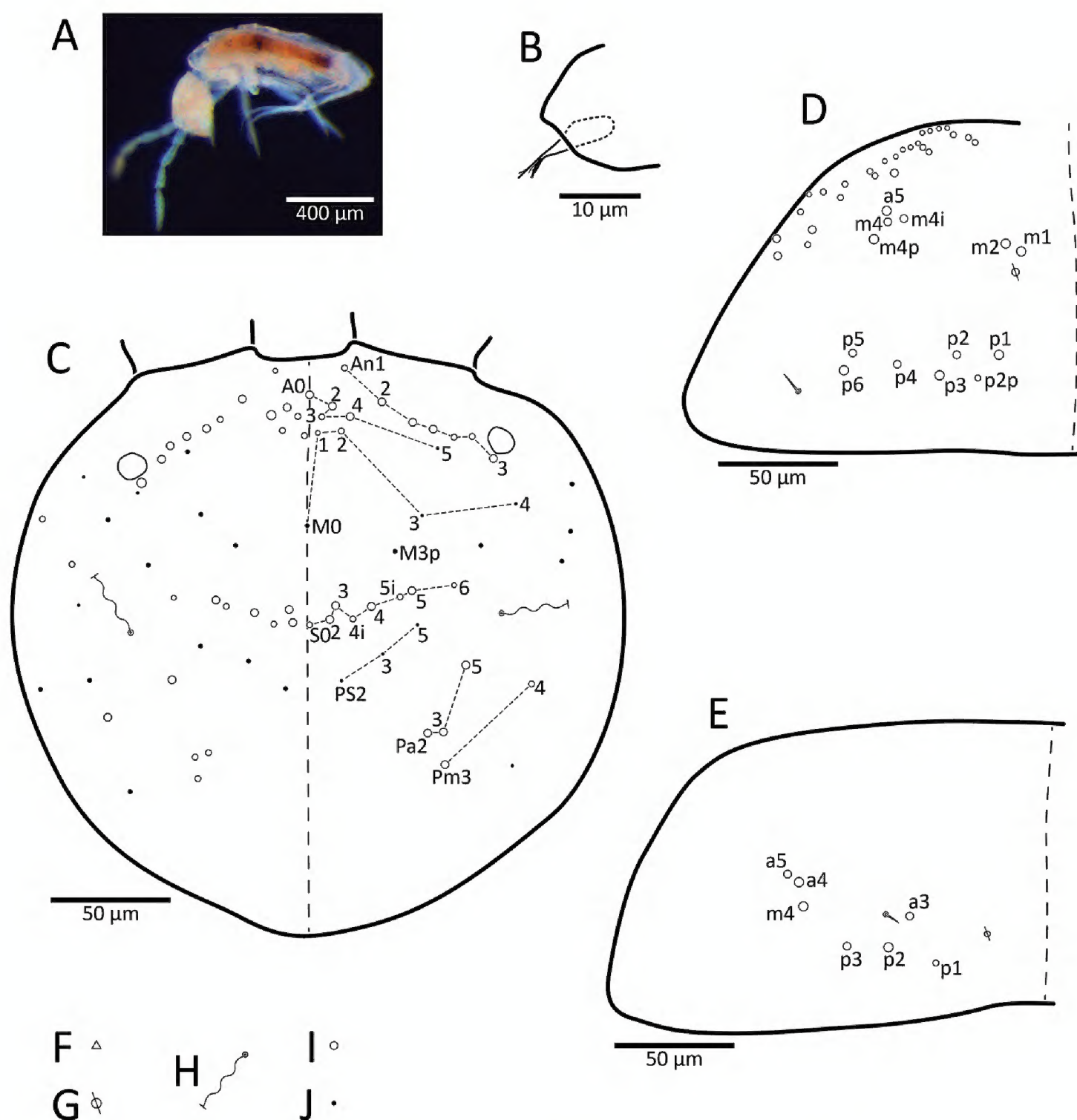


Figure 5. *Heteromurus* (*Heteromurtrella*) *nitens*. **A** habitus (INHS Acc. 567,401) **B** pin sensillum on Ant. IV **C–E** dorsal chaetotaxy: **C** head **D** mesothorax **E** metathorax **F–J** symbols used in illustrations: **F** fan-shaped ciliate microseta associated with bothriotricha **G** pseudopore **H** bothriotricha **I** macroseta **J** meso- or microseta.

M series; row S with 8 Mc, element S1 absent; row Ps with mc Ps2, Ps3, and Ps5; 5 posterior Mc present.

Dorsal body chaetotaxy. Dorsal chaetotaxy of Th. II as in Figure 5D: anterior and medial rows with Mc a5, M1, M2, M4, M4i, M4p; posterior row with 7 Mc. Dorsal chaetotaxy of Th. III as in Figure 5E: with Mc a3, a4, a5, m4, p1, p2 and p3. Dorsal chaetotaxy of Abd. I (Fig. 6A) with 3 Mc (m2, m3, m4). Dorsal chaetotaxy of Abd. II (Fig. 6B) with 2 Mc. Dorsal chaetotaxy of Abd. III (Fig. 6C) with Mc m3 and pm6 present. Dorsal chaetotaxy of Abd. IV (Fig. 6D) with 4 inner Mc; mc T3, ciliate.

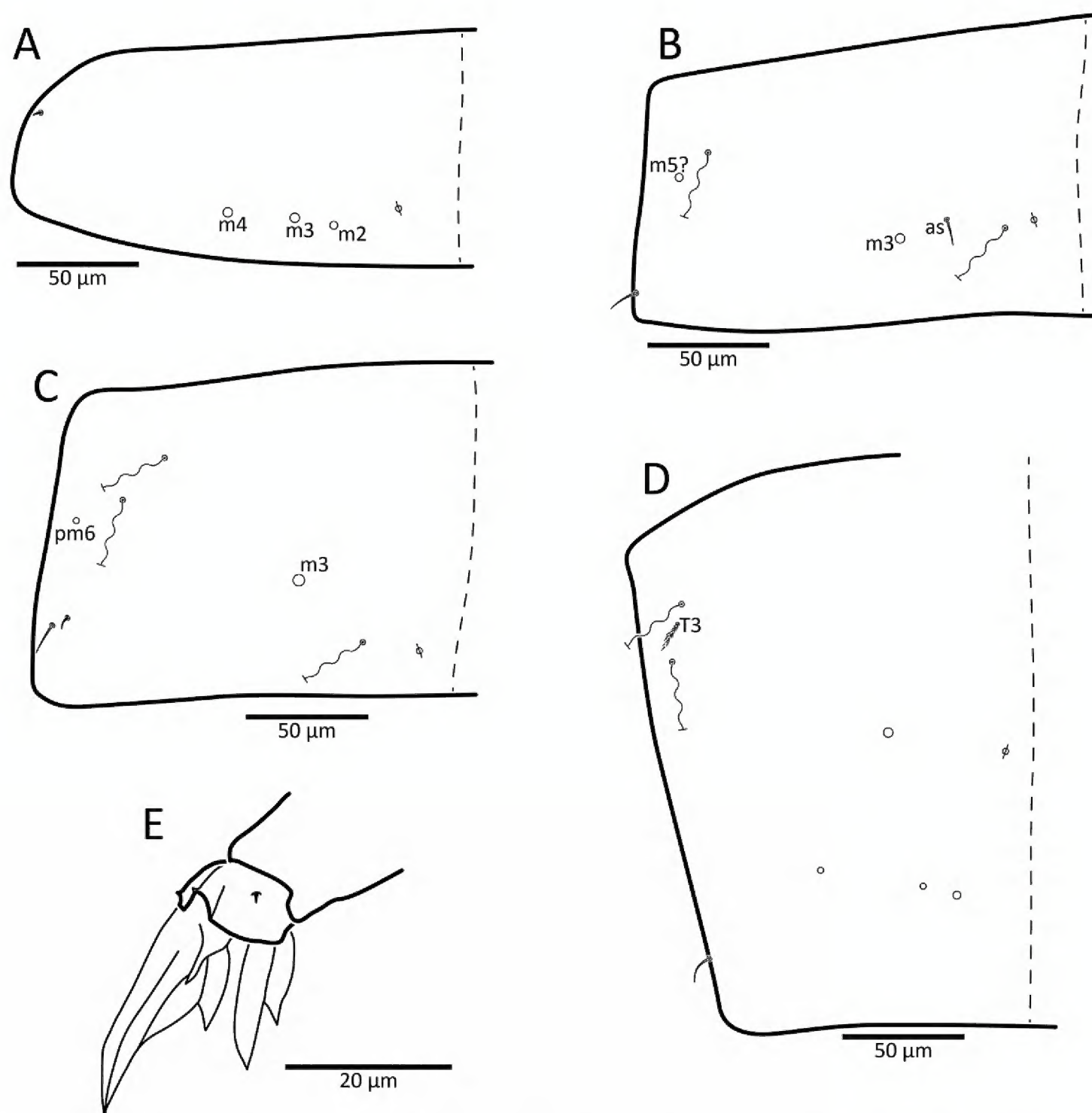


Figure 6. *Heteromurus* (*Heteromurtrella*) *nitens*. **A–D** dorsal chaetotaxy: **A** Abd. I **B** Abd. II **C** Abd. III **D** Abd. IV **E** hind claw complex.

Remarks. The chaetotaxy of the single individual collected (an adult female), is identical to that described for *H. nitens* from the Kingdom of Tonga by Yosii (1964). The individual from Galápagos differs from Yosii's (1964) description only in claw morphology, our specimen lacks the inner unpaired ungual tooth (Fig. 6E). This is the first record of the genus *Heteromurus* from the Galápagos Islands.

The description above is intended to supplement the original description by Yosii (1964) with detailed descriptions and illustrations of dorsal head and body chaetotaxy. Most scales and setae had fallen off our specimen during transport making it difficult to differentiate elements (i.e., scales, sensilla, microsetae). Therefore, the mc on Th. II–Abd. IV are not illustrated. Some sensilla may have also been omitted from the illustrations if not visible on the specimen.

This species' peculiar distribution (reported from Tonga and Galápagos) indicates its range extends across the Pacific Ocean and may occur on other Pacific Islands. The difference in number of inner ungual teeth and vast geographical distance separating the populations of Tonga and Galápagos hint at a species level differentiation. However, in view of the general morphological similarity and a lack of sufficient material, we have chosen not to erect a new name for this single individual.

Distribution. 'Eua Island, Kingdom of Tonga (Yosii 1964) and Isabela Island, Galápagos, Ecuador (new record).

Material examined. Ecuador, Galápagos, Isabela Island: 1 ♀ on slide, La Cueva de Sucre, 21.iii.2014 (G. Hoese), INHS Acc. 567,401.

Lepidocyrtus nigrosetosus Folsom, 1927

Figs 7–12

= *Lepidocyrtus leleupi* Jacquemart, 1976: 145, **syn. n.**

Description. *Size.* Up to 2.6 mm

Color pattern. Background color white or light orange, with dark purple pigment limited to Ant. III-IV, latero-posterior margin of Th. II, lateral margin of Th. III and meso- and metathoracic coxae. Some individuals have an additional irregular purple spot on the base of the furcula, others have no pigment at all, except for the antennae. The black or dark brown look of living specimens is produced by the thick covering of black or dark brown scales (Fig. 7A).

Appendicular scales distribution. Dorsally on Ant. I, femur on middle and hind legs and ventral face of furcula. Scales absent from Ant. II-IV, fore legs, ventral tube and dorsal face of manubrium.

Head. Apical bulb on Ant. IV absent. Dorsal chaetotaxy of the head as in Figures 7B,C: Row An with 7-12 Mc; anterior Mc A0 and A2 present, relatively small but with differentiated sockets, and inserted among a group of enlarged fusiform elements field normally including only Mc A0 (Fig. 7B; fig. 2 in Jacquemart 1976), all other anterior Mc absent; posterior Mc absent, element Ps5 enlarged and fusiform; postocular bothriotrix displaced laterally and inserted behind eyes E and F. Prelabral and all labral setae smooth. Basal seta of outer maxillary palp smooth, subequal to terminal appendage; sublobal plate with 3 seta-like appendages and 1 minute, spine-like appendage on dorsal edge. Lateral appendage on labial papilla E curved anteriorly and short, not reaching tip of papilla. Labial palp with 5 smooth proximal setae. Labial triangle formula as m1M2rEL1L2, A1-5: m1 sometimes coarsely ciliate and always shorter than M2; r short, smooth and conic, sensilla-like (Fig. 8A). Anterior row of post-labial setae smooth or minutely denticulate; setae on posterior rows coarsely ciliate (Fig. 8B, C); cephalic groove with 5-6 +5-6 setae, anterior most seta smooth, setae becoming more coarsely ciliate from anterior to posterior rows; postlabial group C with 1-4 setae; modified post-labial setae 2-3, short, conic and smooth, similar to labial seta r, inserted among lateral columns.

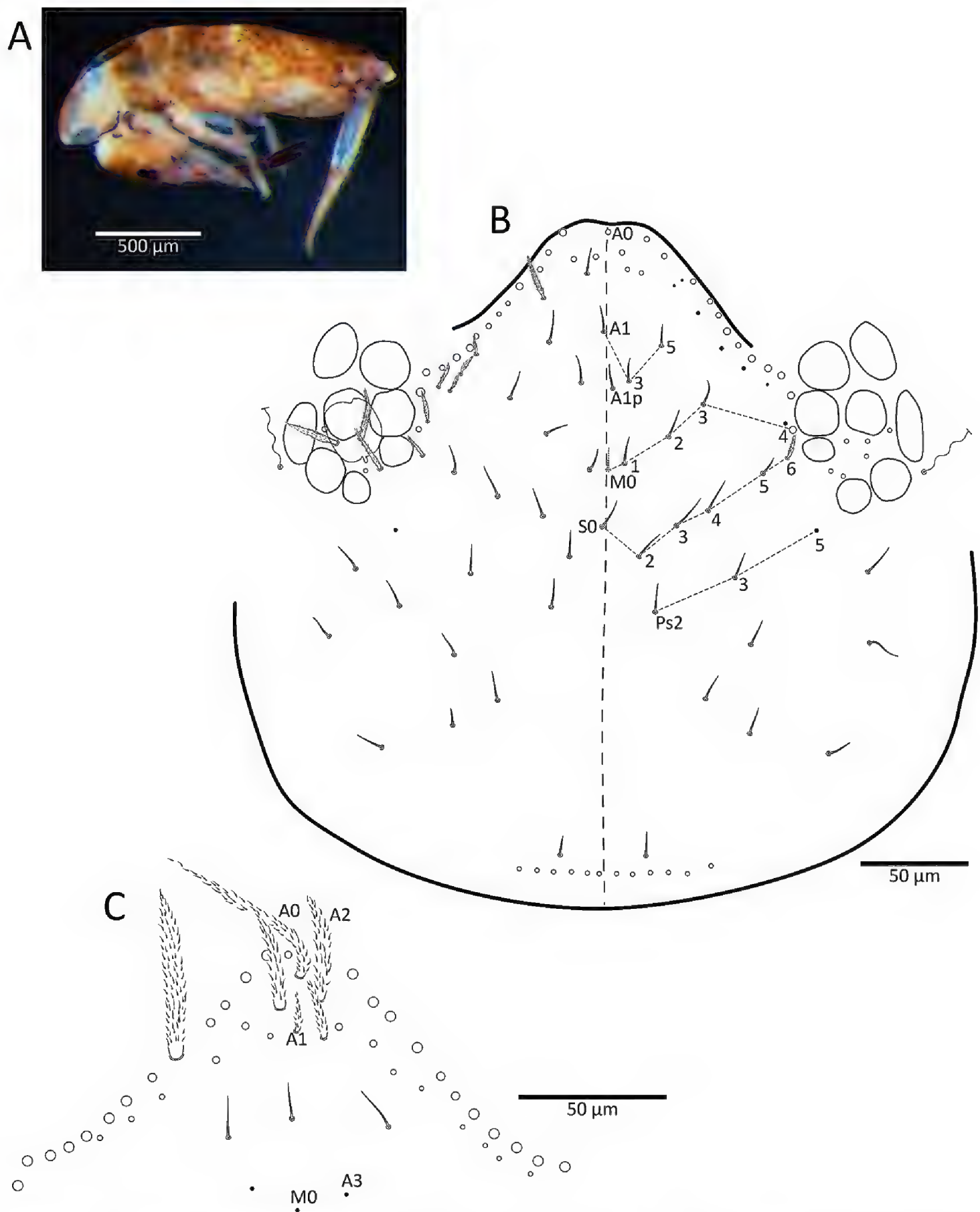


Figure 7. *Lepidocyrtus nigrosetosus*. **A** habitus (INHS Acc. 567,402) **B** dorsal chaetotaxy of head **C** detail of anterior chaetotaxy of head.

Dorsal body chaetotaxy. Dorsal macrosetae formula 00/0233+1+6. Dorsal S-seta 11/011n3; S-microseta 10/10100. Mesothoracic hood produced, anteriorly rounded, partially or completely shadowing head. Meso- and metathoracic chaetotaxy normal, with neither Th. II polychaetosis nor Th. III reductions. Chaetotaxy of Abd. I normal, with a6 present and 11 posterior setae. Abd. II (Fig. 9A, B) with all supplementary

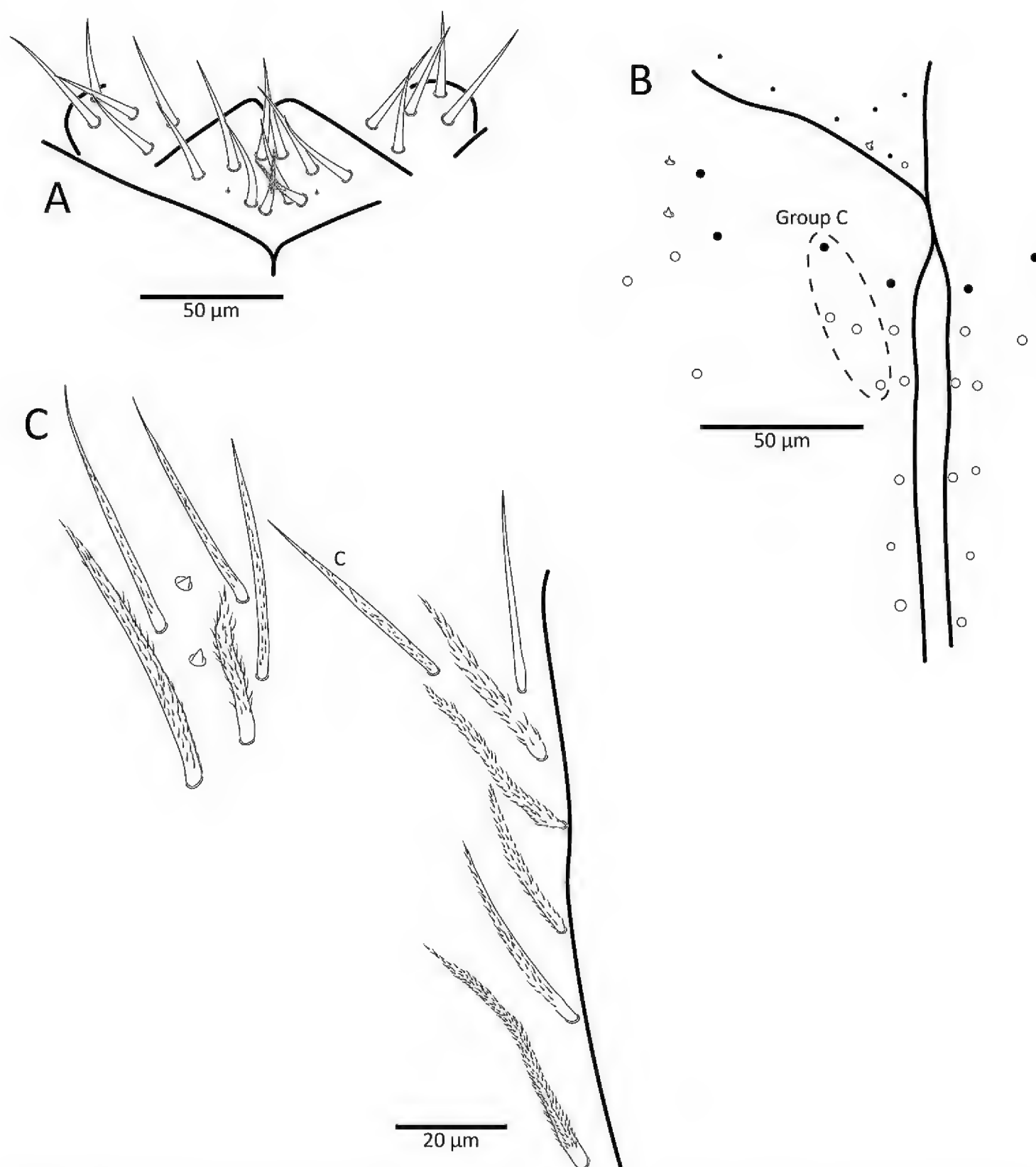


Figure 8. *Lepidocyrtus nigrosetosus*. **A** labial triangle **B** postlabial chaetotaxy **C** detail of postlabial chaetotaxy.

setae fan-shaped; a2 and a6 fusiform and finely ciliate in larger individuals, normal smooth setae in smaller individuals; a3 well anterior and not reaching sensillum as; as subequal to or shorter than a3; Mc m3 and m5 present; p4, m4, and p5 smooth; elements a2p, m3e, m4i and p5p absent. Abd. III (Fig. 9C) with all supplementary setae fan-shaped; a2, a6 and am6 fan-shaped; a3 well anterior and not reaching as; as shorter than a3 and m3; Mc pm6, p6 and p7 present; mc p3, m4, p5 and S-microseta d2 present; a7 smooth or very finely denticulate, displaced laterally, not reaching am6. Abd. IV (Fig. 10) with inner Mc B4, B5, B6 and C1; all supplementary setae of both-

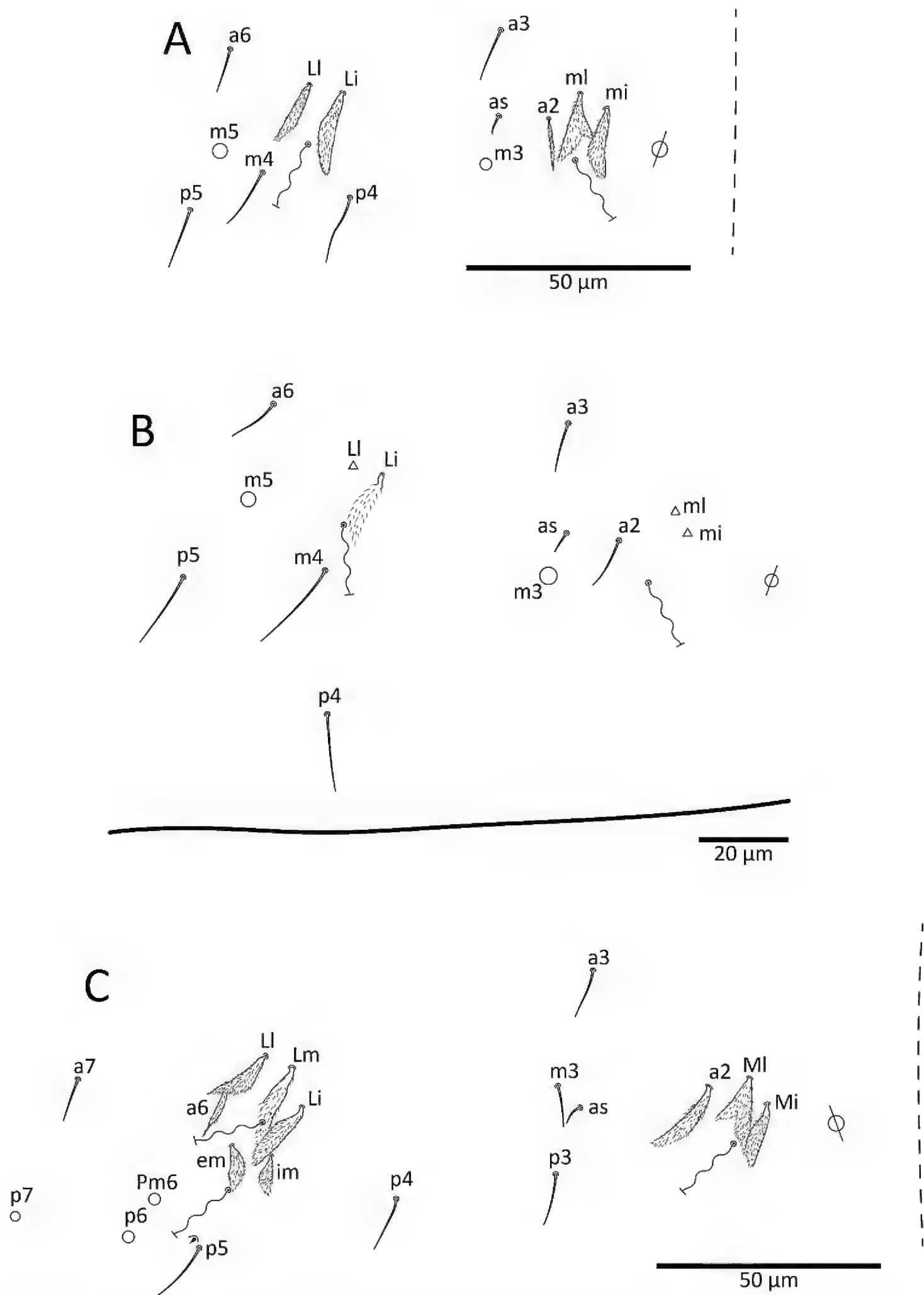


Figure 9. *Lepidocyrtus nigrosetosus*. **A–C** dorsal chaetotaxy: **A** Abd. II **B** Abd. II of *L. leleupi* paratype; **C** Abd. III.

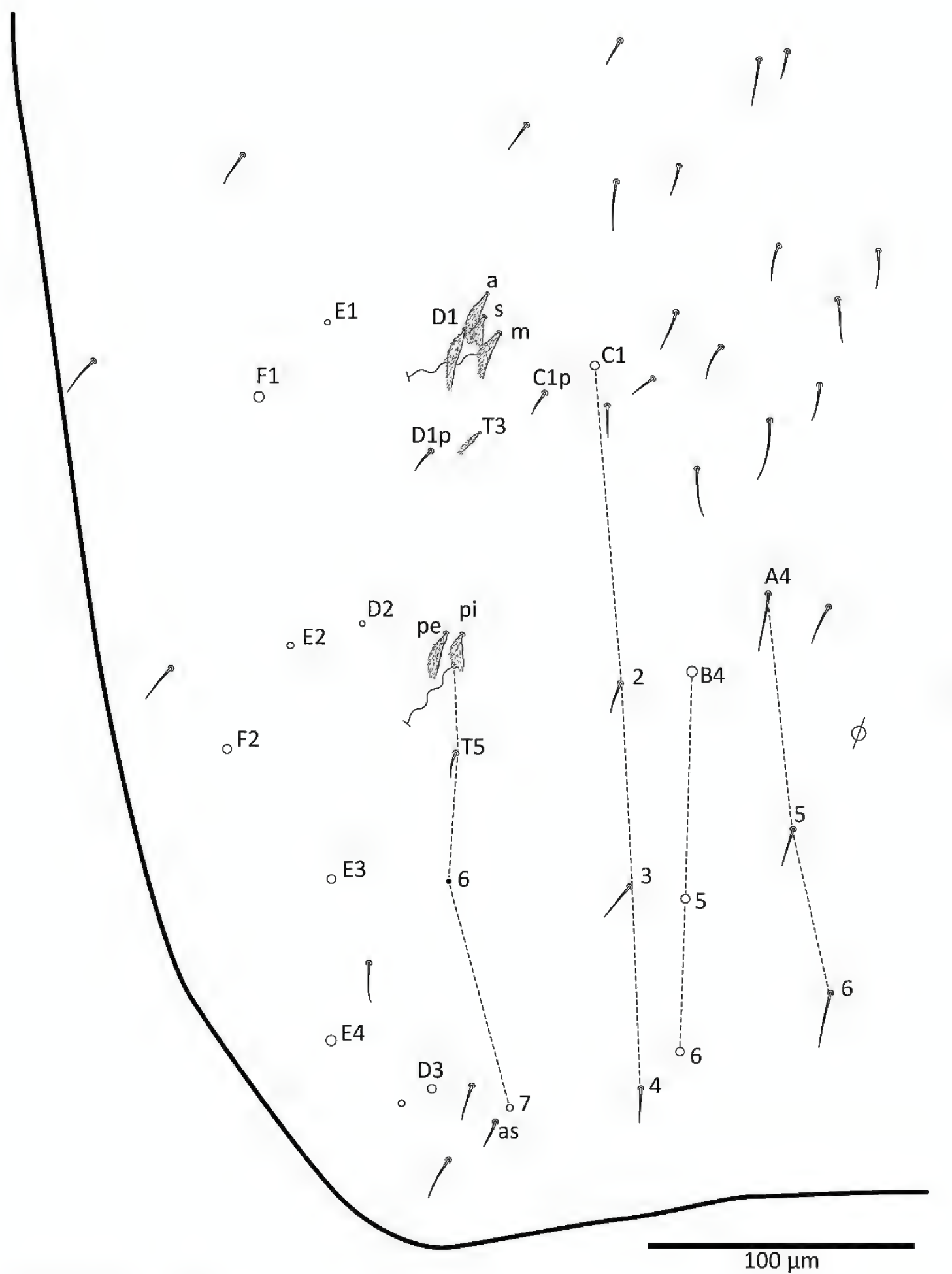


Figure 10. *Lepidocyrtus nigrosetosus*, dorsal chaetotaxy of Abd. IV.

riotrichal complex fan-shaped; mc s present (Fig. 11B); bothriotricha T2 and T4 well separated; mc T3 and D1p subequal, short, displaced anteriorly, closer to T2 than T4, and not reaching Pe or Pi; lateral Mc D3, E2, E3, F1, F2, F3 present (Fig. 11A); posterior setae 10–12.

Legs. Trochanteral organ with up to 41 setae. Tenent hair spatulate on all legs. Unguis with 3–4 inner teeth, distal unpaired tooth sometimes absent; all teeth small; proximal unpaired tooth well separated from basal paired teeth. Fore and middle unguiculi relatively short, strongly truncate, with well marked inner tooth and weakly serrate posterior edge; hind unguiculus usually lanceolate or weakly truncate, rarely strongly truncate, inner tooth absent or weakly delineated; hind unguiculus always clearly longer (surpassing inner proximal unpaired ungual tooth) than fore and middle unguiculi (barely reaching inner proximal unpaired tooth).

Ventral tube. All faces covered by many finely ciliate setae; posterior face with 1+1 smooth setae on distal margin in addition to ciliate setae (Fig. 11C)

Furcula. Manubrium and dens without smooth setae. Basal tubercle of dens apically rounded, somewhat asymmetrical. Mucro with apical tooth slightly longer than basal tooth. Mucronal spine with minute basal denticles.

Remarks. This species is characterized by the enlarged, rounded mesothoracic hood, absence of dorsal head Mc posterior to A2, smooth labial setae, absence of seta m3e on Abd. II, four inner Mc on Abd. IV, heteromorphic unguiculi (truncate on fore and middle legs, lanceolate or weakly truncate on hind leg), and a rounded but somewhat asymmetric tubercle on the dens.

As pointed out by Bernard et al. (2015) the large bodied members of the *L. nigrosetosus* species group (*L. nigrosetosus*, *L. immaculatus* Folsom, 1932, *L. leleupi* Jacquemart, 1976 and *L. geayides* Denis, 1931) are very similar and difficult to distinguish. Bernard et al. (2015) suggested that *L. leleupi*, originally described from the island of Santa Cruz in the Galápagos, was likely to be a junior synonym of *L. nigrosetosus*. Our collections of *Lepidocyrtus* from Santa Cruz fit the color pattern description of *L. leleupi* and at first the specimens were identified as that species, but evaluation of other morphological characters showed the specimens to fit the range of variation reported for *L. nigrosetosus* (Mari Mutt 1986). To confirm these observations we studied the type series of *L. leleupi* deposited in the Royal Belgian Institute of Natural Sciences in Brussels, Belgium.

The type series of *L. leleupi* comprises the holotype, 11 paratypes and 4 additional specimens mounted on slides. The slide labeled holotype holds two individuals. Jacquemart (1976) did not specify which of the two individuals was the holotype, hence here we designate an individual as the holotype (arrow in Figure 12). The holotype and other members of the type series *L. leleupi* lack mc m3e on Abd. II (Fig. 9B) and show the same range of morphological variation seen in specimens of *L. nigrosetosus* from Puerto Rico. For this reason we consider *L. leleupi* a junior synonym of *L. nigrosetosus*. This makes *L. nigrosetosus* the most geographically widespread member of the genus in the Neotropical region (Soto-Adames and Anderson in press).

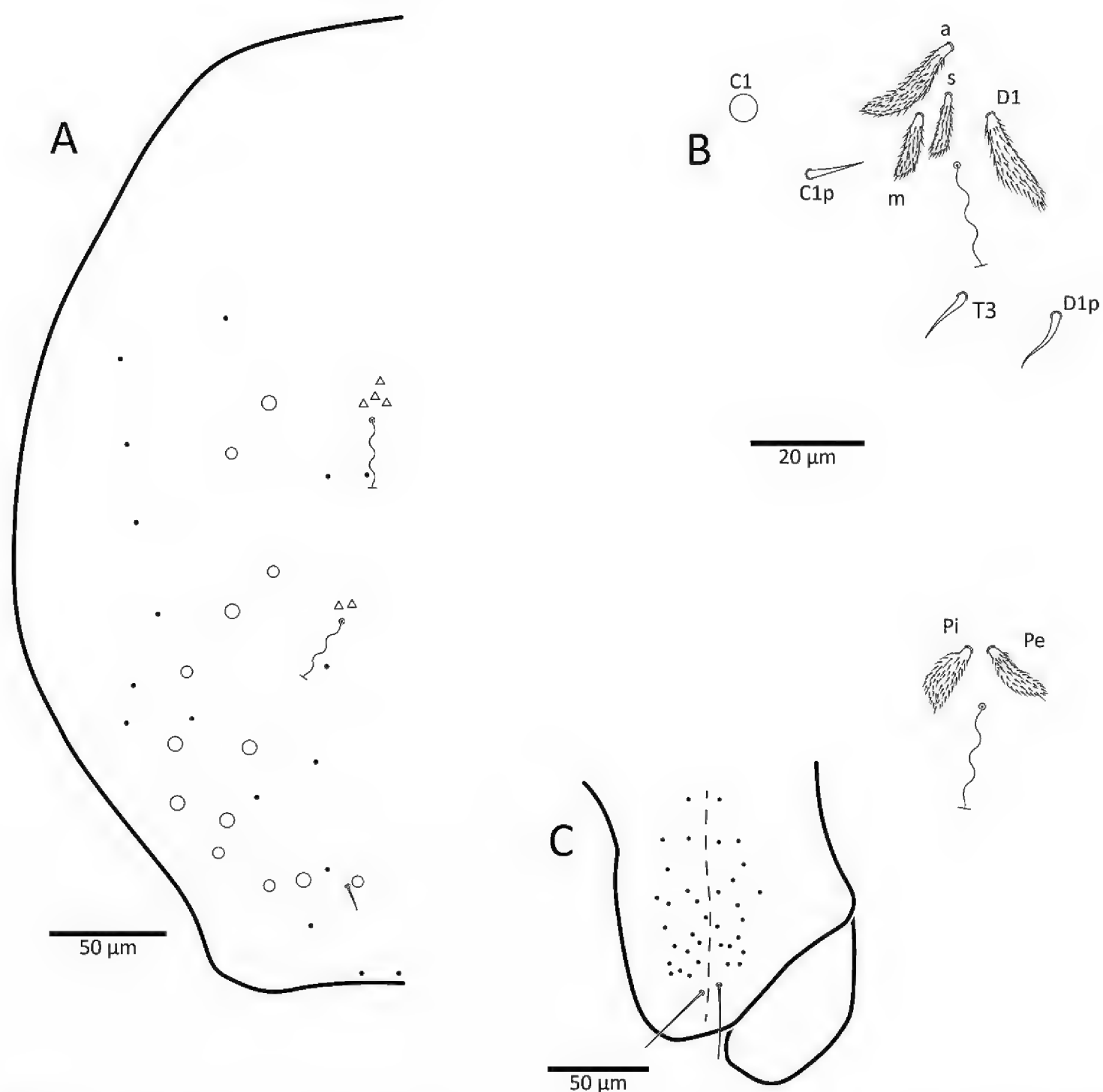


Figure 11. *Lepidocyrtus nigrosetosus*. **A** dorso-lateral chaetotaxy of Abd. IV **B** detail of bothriotricha complex chaetotaxy of Abd. IV **C** posterior face of collophore.

Distribution. Galápagos (new record), Puerto Rico, Colombia, Jamaica (Mari Mutt and Bellinger 1990), St. Thomas US Virgin Islands (Soto-Adames 2002a, 2002b), Brazil (Bellini and Zeppelini 2009), Nevis (Soto-Adames and Anderson in press).

Material examined. Ecuador, Galápagos, Santa Cruz Island: 1♀ on slide, Cueva Cascajo, wet breakdown with leaf litter on entrance floor, 9.iii.2014 (S. Taylor, J. Jacoby and M. Sutton), GLP-030, INHS Acc. 567,402; 1♀ on slide, Cueva Cañón, mossy breakdown near entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-032, INHS Acc. 567,403; 1 on slide, Cueva Aguirre, leaf litter, entrance, 10.iii.2014 (G. Hoese), GLP-046, INHS Acc. 567,404; 1♀ on slide, Cueva Chato 1, on wet soil near entrance, 8.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R.



Figure 12. *Lepidocyrtus leleupi* holotype (arrow).

Toomey), GLP-075, INHS Acc. 567,405; 1 on slide, Cueva Chato 1, on wet soil near entrance, 8.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-075, CDRS; 1♂ on slide, Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, INHS Acc. 567,406; 1 on slide, Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, CDRS; 2 on slides, Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, INHS Acc. 567,407 & 567,408.

Lepidocyrtus leleupi Holotype, Galápagos, Santa Cruz, humus forêt humile, 200m, xi.1964; 11 paratypes with same collection information as holotype; 2 other slides with same collection locality, but 22.x.1964; 2 slides Galápagos, Santa Cruz, Station 92B, 17.ii.1974, I.G. 24.965, RBINS.

Pseudosinella intermixta (Folsom, 1924)

Fig. 13

Descriptive notes of type specimen. Slide mounted syntype is 0.63 mm in length (Fig. 13A). Unguis with 3 inner teeth: 2 minute basal paired teeth and 1 large unpaired distal tooth (Fig. 13B). Dorsal head Mc A0, A2, A3, and M2 (S) present; Pa5 absent. Th. II with 1 Mc. Th. III without Mc.

Remarks. *Pseudosinella intermixta*, originally described by Folsom (1924) from material collected on Baltra Island (as South Seymore Island), is the only member of the genus with 3+3 eyes, an apical Ant. IV bulb, with head Mc M2, 1 Mc on Th. II, and without Mc on Th. III. Folsom's species is very similar to *P. stewartpecki* sp. n. described below, but can be separated by the presence in *P. intermixta* of head Mc M2 and an enlarged unpaired ungual tooth that is larger than both inner paired teeth.

Folsom's (1924) description of *P. intermixta* is relatively incomplete, lacking details for many important characters, thus it was necessary to revisit the type material to determine if our specimens (described below as *P. stewartpecki* sp. n.) differed from

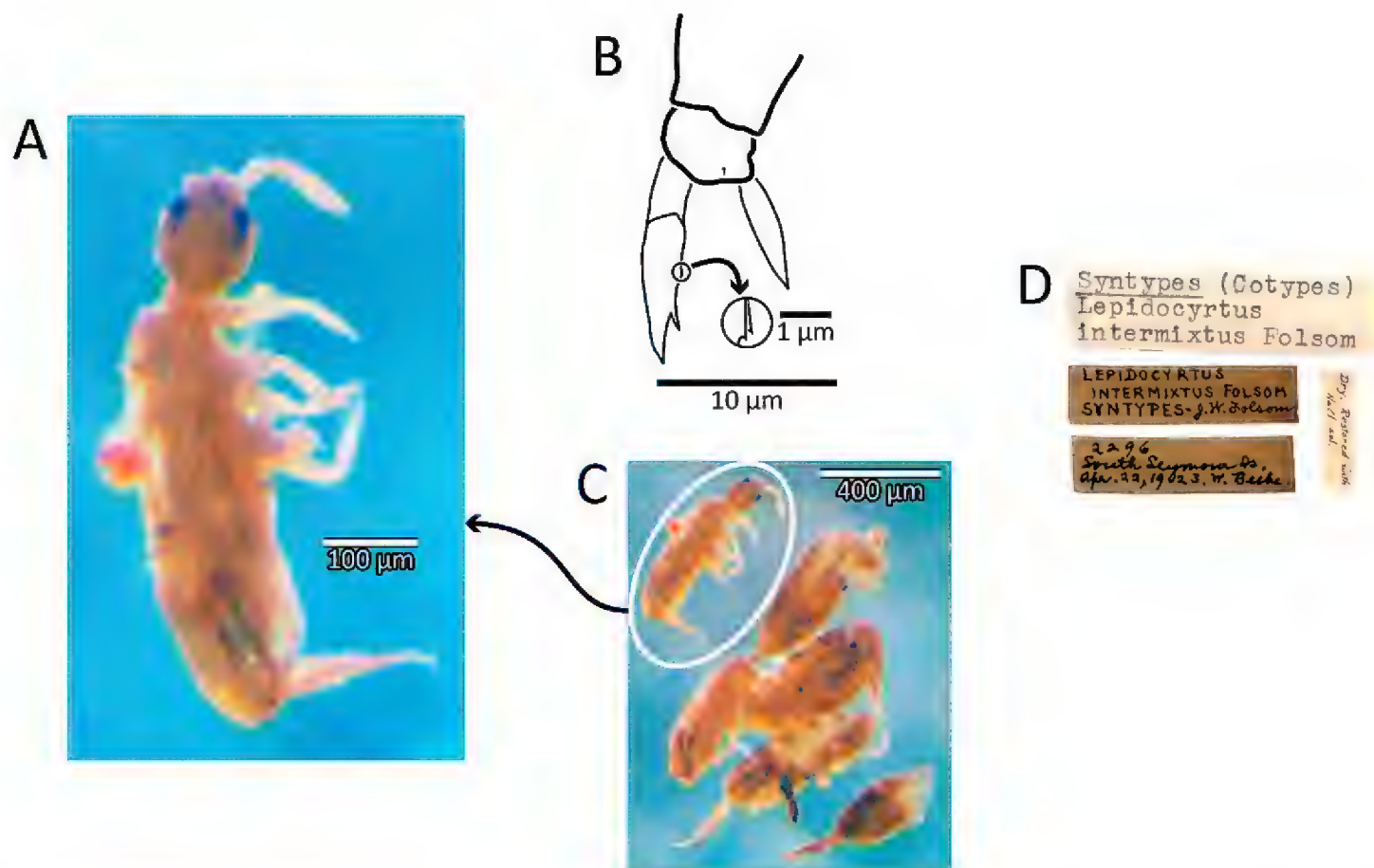


Figure 13. *Pseudosinella intermixta* syntypes. **A** syntype specimen chosen for slide mount (INHS Acc. 567,409) **B** hind claw complex **C** detail of preservation condition of syntypes in ethanol **D** original labels in vial.

P. intermixta. The syntypes, stored in ethanol with labels (Fig. 13C, D), were in extremely poor condition. Despite their poor condition, after slide mounting the most complete specimen (Fig. 13A) we were able to supplement Folsom's (1924) description with the few additional characters provided above.

Folsom (1924) described and illustrated *P. intermixta* with only 2 subequal inner teeth on the unguis. However, the mounted syntype clearly has 3 inner teeth: 2 minute paired teeth and 1 large unpaired distal tooth (Fig. 13B). Due to old age and poor preservation, dorsal chaetotaxy is mostly obscured on the mounted type specimen, but the head clearly carries Mc M2.

Distribution. Baltra Island, Galápagos, Ecuador (Folsom 1924).

Material examined. *Syntypes*, 1 on slide, 5 in vial, Ecuador, Galápagos, Baltra (South Seymour) Island, Apr. 22, 1923, coll. W. Beebe, 2296, dry restored with NaCl sol.; INHS Acc. 567,409 (slide mounted syntype) & 567,410 (syntypes in alcohol).

***Pseudosinella stewartpecki* Katz, Soto-Adames & Taylor, sp. n.**

<http://zoobank.org/A1A125AB-B9B2-41E5-863F-7A17BBA70C63>

Figs 14–17

Etymology. A patronym honoring Stewart B. Peck (Carleton University, Ottawa) whose work in caves and other habitats has done much to increase our understand-

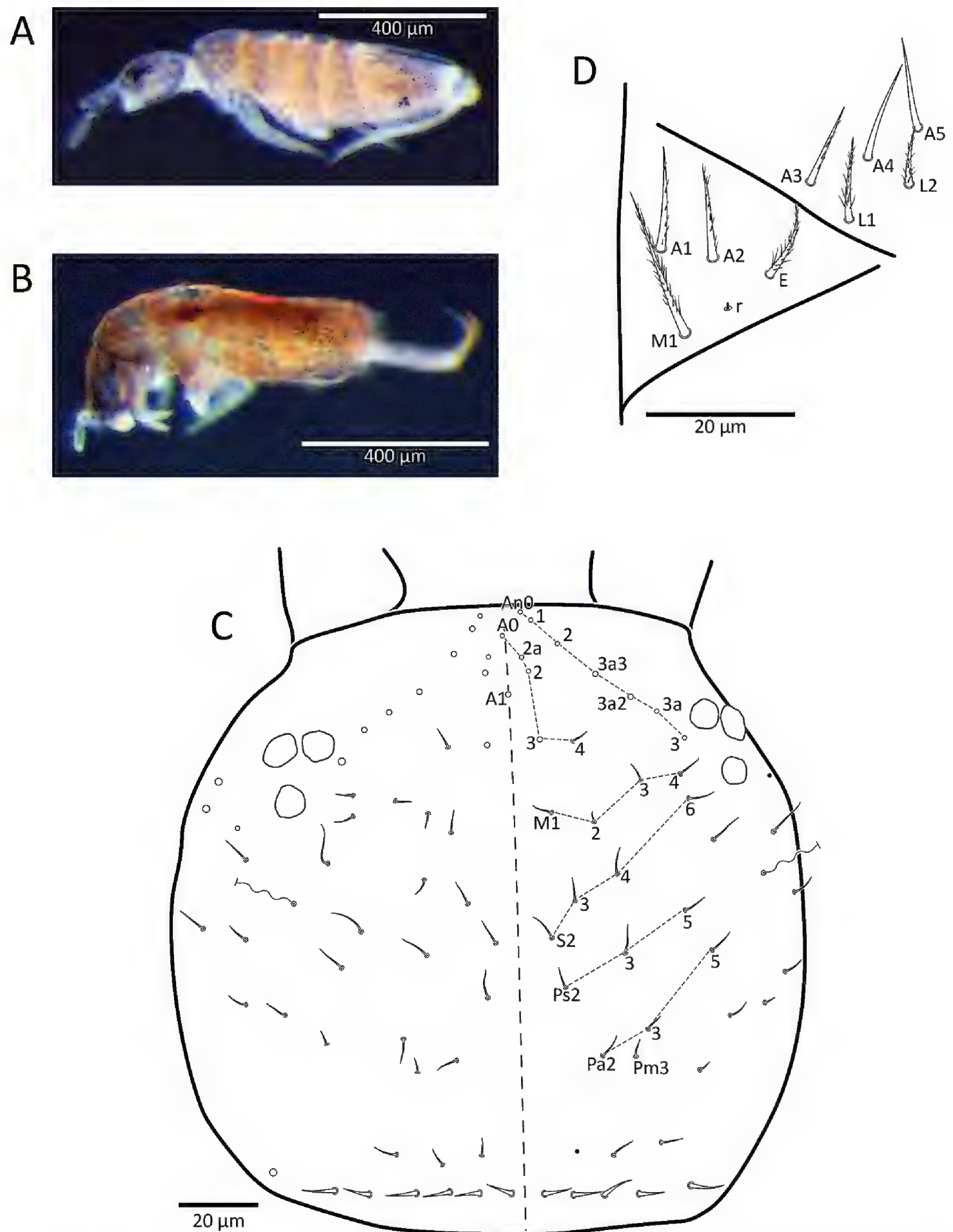


Figure 14. *Pseudosinella stewartpecki* sp. n. **A–B** habitus (INHS Acc. 567,418 & 567,419) **C** dorsal chaetotaxy of head **D** labial triangle.

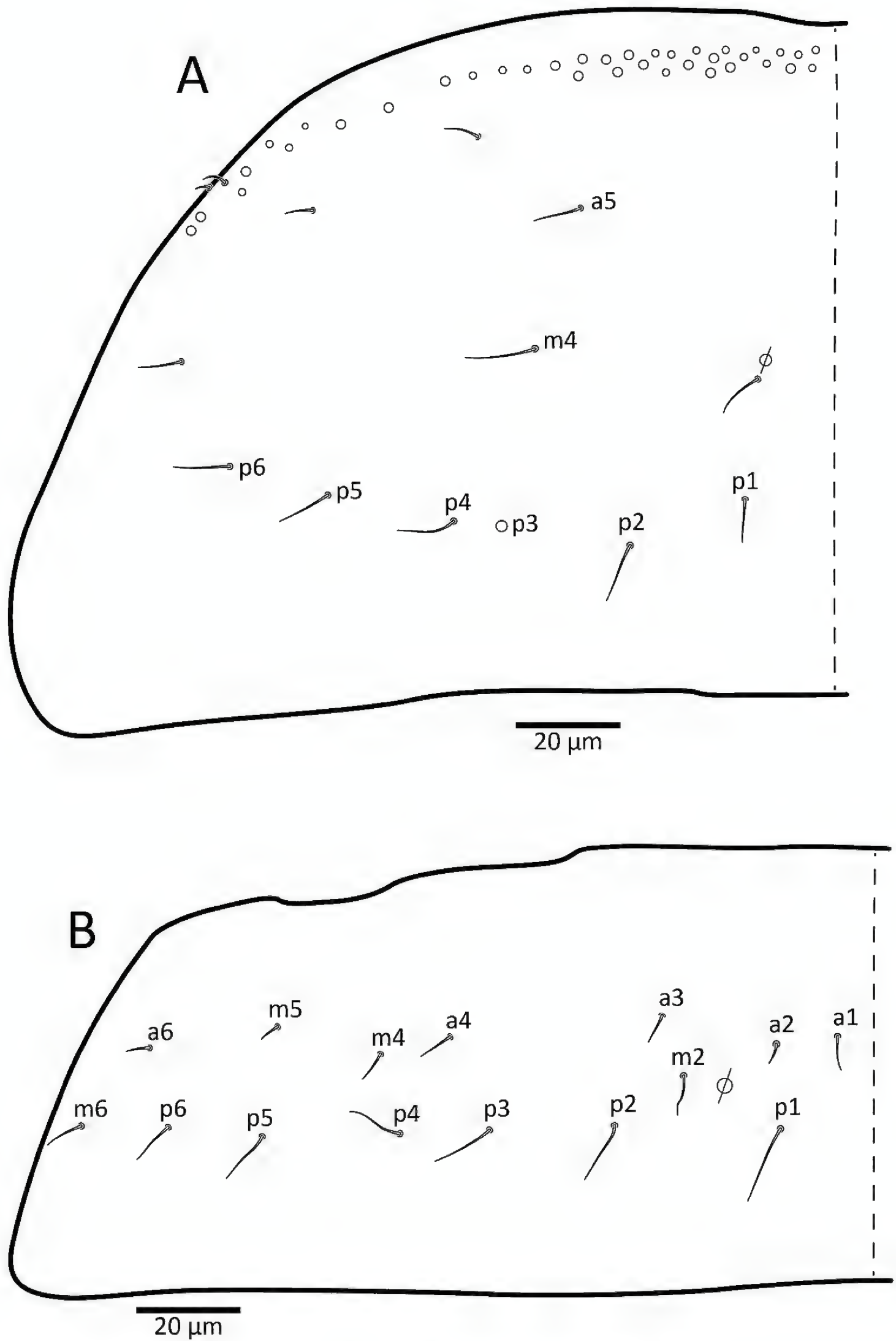


Figure 15. *Pseudosinella stewartpecki* sp. n. **A–B** dorsal chaetotaxy: **A** Th. II **B** Th. III.

ing of invertebrate biodiversity in the Galápagos Islands and throughout the Western Hemisphere.

Type material. *Holotype*, ♂ on slide, Ecuador, Galápagos, Santa Cruz Island: La Llegada, leaf litter from entrance, 12.iii.2014 (C. Plowman, D. Butler and G. Hoese), GLP-095, INHS Acc. 567,414.

Paratypes, Ecuador, Galápagos, Santa Cruz Island: 2♂ on slides, La Llegada, leaf litter from entrance, 12.iii.2014 (C. Plowman, D. Butler and G. Hoese), GLP-095, INHS Acc. 567,415 & 467,416; 2♀ on slides, La Llegada, leaf litter from entrance, 12.iii.2014 (C. Plowman, D. Butler and G. Hoese), GLP-095, INHS Acc. 567,417 & 467,418; 2 on slides, La Llegada, leaf litter from entrance, 12.iii.2014 (C. Plowman, D. Butler and G. Hoese), GLP-095, INHS Acc. 567,419 & 467,420; 1 on slide, La Llegada, leaf litter from entrance, 12.iii.2014 (C. Plowman, D. Butler and G. Hoese), GLP-095, CDRS.

Description. *Body shape and color pattern.* Maximum body length 1.14mm (♀) and 0.85mm (♂). Body with uniformly light blue pigment and white (rarely light orange) background (Fig. 14A, B).

Appendicular scales distribution. Scales present on head, body and ventral face of furcula. Antennae, legs, ventral tube and dorsal face of furcula without scales.

Head. Apical bulb of Ant. IV simple, membranous. Subapical sense organ acuminate; length subequal to guard sensillum. Sense organ of Ant. III with 2 normal rods; at least 3 additional short, blunt sensilla. Eyes 3+3. Dorsal head Mc (Fig. 14C) A0, A2a, A2 and A3 present, An series with 6+6 Mc (7+7 including An0). Pa5 absent. Prelabral setae weakly ciliate. Proximal labral setae ciliate, medial and distal labral setae smooth. Distal margin of labrum smooth. Outer maxillary lobe with basal and distal setae smooth and subequal. Sublobal plate with 3 appendages, subequal in length. Lateral appendage of labial papilla E reaching tip of papilla. Proximal labial setae smooth. Labial triangle setae formula: M1rEL1L2A1-3A4-5; A1-3 serrate, A4-5 smooth; r minute, smooth and conical; all other posterior setae ciliate (Fig. 14D). Postlabial setae ciliate; 4 setae and 4 scales along ventral groove; modified setae absent.

Body dorsal chaetotaxy. Th. II with Mc P3 present (Fig. 15A): polychaetosis absent; hood not developed. Th. III without Mc (Fig. 15B). Abd. I with 11 posterior mc, a6 present (Fig. 16A). Abd. II (Fig. 16B) with 2 Mc (m3, m5); all supplementary mc associated with bothriotricha acuminate and smooth; mc a2p, m4i, p5p, Lm, and Ll absent; seta a3 anterior to and reaching sensillum as. Abd. III (Fig. 16C) with 2 Mc (pm6, p6); all supplementary mc associated with bothriotricha acuminate and smooth; sensillum d2 and mc c3 and Ll absent; seta a3 anterior and reaching sensillum as; as less than half the length of m3; seta a7 anterior to im and em, reaching am6. Abd. IV (Fig. 17A) with 2 inner (B5, B6) and 7 lateral Mc (T6, D2-3, E2-4, F1); E1 a mc; 1 additional posterior-lateral Mc of uncertain homology present; supplementary mc associated with bothriotricha acuminate and smooth, mc s, a, and Pe absent; mc T3 anterior to and not reaching D1p; mc F2 in row with D2 and E2; posterior setae absent. Scales present on ventral face of furcula. Dens tubercle absent. Mucro with sub-apical tooth slightly longer than apical; basal spine smooth.



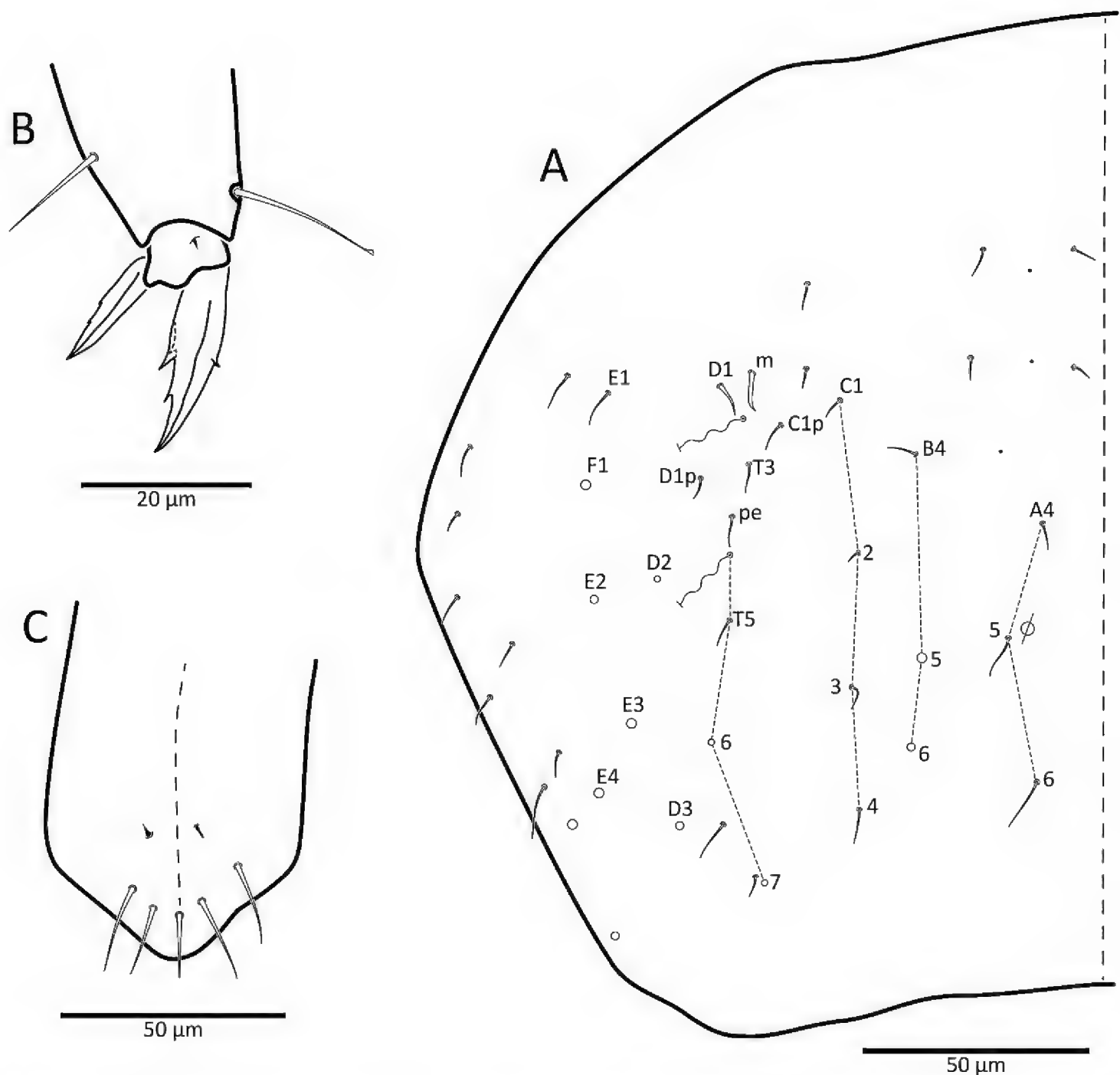


Figure 17. *Pseudosinella stewartpecki* sp. n. **A** dorsal chaetotaxy of Abd. IV **B** hind claw complex **C** posterior face of collophore.

Legs. Trochanteral organ with 5 setae on all specimens when visible. Metatibiotarsi without outstanding posterior blunt setae. Tenent hair spatulate. Unguis with 3 inner teeth: 1 distal unpaired tooth and 2 basal paired teeth with 1 large tooth and 1 small tooth, the latter significantly smaller than distal unpaired tooth. Unguiculus lanceolate with at least 2 or more minute teeth on all legs (Fig. 17B).

Ventral tube. Anterior face with 4+4 or 5+5 ciliate setae; lateral flaps with 5+5 or 6+6 smooth setae; posterior face (Fig. 17C) with 2+2 smooth lateral setae, 1 smooth medial seta, and 1+1 minute conical microsensilla.

Remarks. *Pseudosinella stewartpecki* sp. n. is the only member of the genus with 3+3 eyes, an apical antennal bulb, head series M and S without Mc, with 1 Mc on Th. II, and without Mc on Th. III. This new species is most similar to *P. intermixta*, also described from the Galápagos Islands (Folsom 1924). However, *P. stewartpecki* sp. n. lacks head Mc in rows M and S, and the unpaired inner tooth of the unguis is smaller

than the largest of the two inner paired teeth (Fig. 17B), whereas in *P. intermixta*, head Mc M2 is present and the unpaired inner tooth is substantially larger than both paired teeth (Fig. 13B). *Pseudosinella intermixta* was collected on Baltra Island, which can be characterized as dry, lowland (maximum elevation of 100m) habitat. *Pseudosinella stewartpecki* sp. n. was collected in relatively moist, upland (251 m) habitat on Santa Cruz Island. These differences, in morphology and habitat, are sufficient for the separation *P. intermixta* and *P. stewartpecki* sp. n.

Distribution. Santa Cruz Island, Galápagos, Ecuador.

***Pseudosinella vulcana* Katz, Soto-Adames & Taylor, sp. n.**

<http://zoobank.org/93AB0B74-D429-4E08-A33E-B4D8E922E222>

Figs 18–20

Etymology. Latin, feminine form, alludes to the shield volcanoes of the Galápagos Islands.

Type material. *Holotype*, ♂ on slide, Ecuador, Galápagos, Santa Cruz Island: Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, INHS Acc. 567,411.

Paratypes, Ecuador, Galápagos, Santa Cruz Island: 1♀ on slide, Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, INHS Acc. 567,412; 1♀ on slide, Cueva Chato 2, drip pool, dark zone, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-090, INHS Acc. 567,413; 1♀ on slide, Cueva Chato 2, drip pool, dark zone, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-090, CDRS.

Description. *Body shape and color pattern.* Maximum body length 0.74mm (♀) and 0.68mm (♂). Body white, without pigment, except for minute black eye spot (Fig. 18A).

Appendicular scales distribution. Scales limited to head, body and ventral face of furcula. Antennae, legs, ventral tube and dorsal face of furcula without scales.

Head. Apical bulb of Ant. IV absent; subapical sense organ clubbed, as large as guard sensillum; additional bulb-like sense organ present within a deep pit. Sense organ of Ant. III with 2 normal rods; at least 2 additional short, blunt sensilla present. Eyes 1+1, each within a minute eye spot. Dorsal head chaetotaxy (Fig. 18B) with 5+5 Mc in An series, in addition to Mc A0, A2, A3, and Pa5. Prelabral setae acuminate and weakly ciliate. Proximal labral setae ciliate, medial and distal labral setae smooth. Distal margin of labrum smooth. Outer maxillary lobe with basal and distal setae smooth and subequal; sublobal plate with 3 seta-like appendages, middle appendage 2' longer and 2' thicker than outer appendage. Lateral appendage of labial papilla E S-shaped, not reaching tip of papilla. Proximal labial setae smooth. Labial triangle setae formula: M1rEL1L2A1-5; A1-5 smooth; r minute, smooth, and conical; all other posterior setae ciliate (Fig. 18C). Postlabial setae ciliate; 3 setae and 4 scales along each side of ventral groove; modified setae absent.

Dorsal body chaetotaxy. Th. II without Mc (Fig. 19A): polychaetosis absent; mesothoracic hood not developed. Th. III without Mc (Fig. 19B). Abd. I (Fig. 19C) with 9

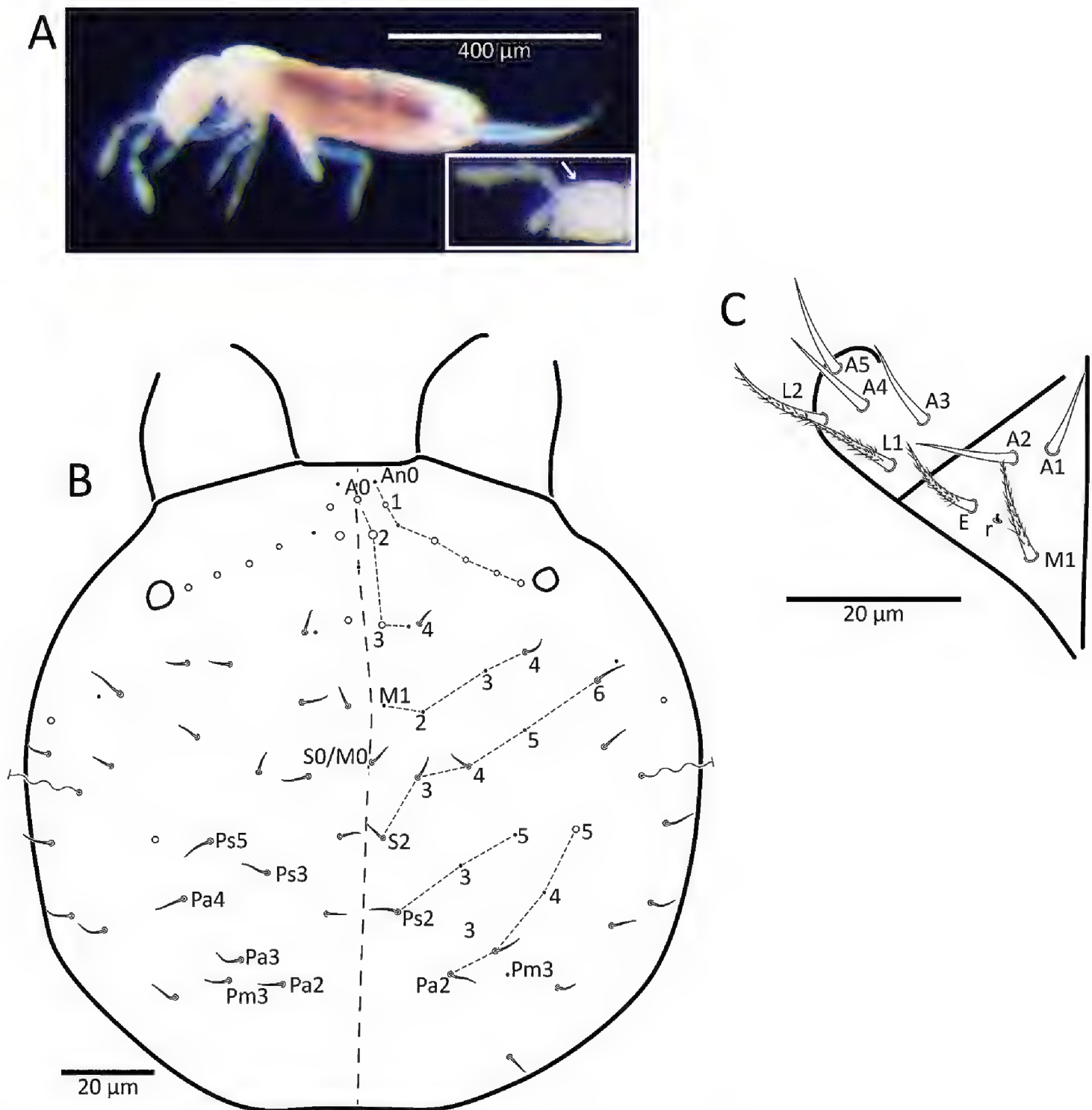


Figure 18. *Pseudosinella vulcana* sp. n. **A** habitus (INHS Acc. 567,412) with detail of eyespot (arrow) on another specimen **B** labial triangle **C** dorsal chaetotaxy of head.

posterior mc; seta a6 absent. Abd. II (Fig. 19D) with 3 Mc (m3, m5, a2); Mc a2 short, thickened distally, with relatively small socket; supplementary setae mi, Li, Ll and m4i associated with bothriotricha m2 and a5 ciliate and weakly fan-shaped/truncate; all other mc acuminate and smooth; mc a2p and Lm, absent; seta a3 external to and half the length of as. Abd. III (Fig. 20A) with 2 Mc (pm6, p6); supplementary mc mi, ml, a2, Li, Lm, im and a6 weakly fan-shaped and ciliate, all other mc smooth; sensillum d2 and mc c3 and Ll absent; seta a3 anterior to and nearly reaching sensillum as; as twice as long as m3; seta a7 posterior to im and em and external to am6. Abd. IV (Fig. 20B) with 2 inner (B5, C1) and 4 lateral Mc (D3, E2, E3, F1); at least 1 additional posterior-lateral Mc of uncertain homology present; supplementary mc associated with bothriotricha weakly fan-shaped and ciliate; seta s present; mc T3 anterior to and not reaching D1p; posterior setae absent.

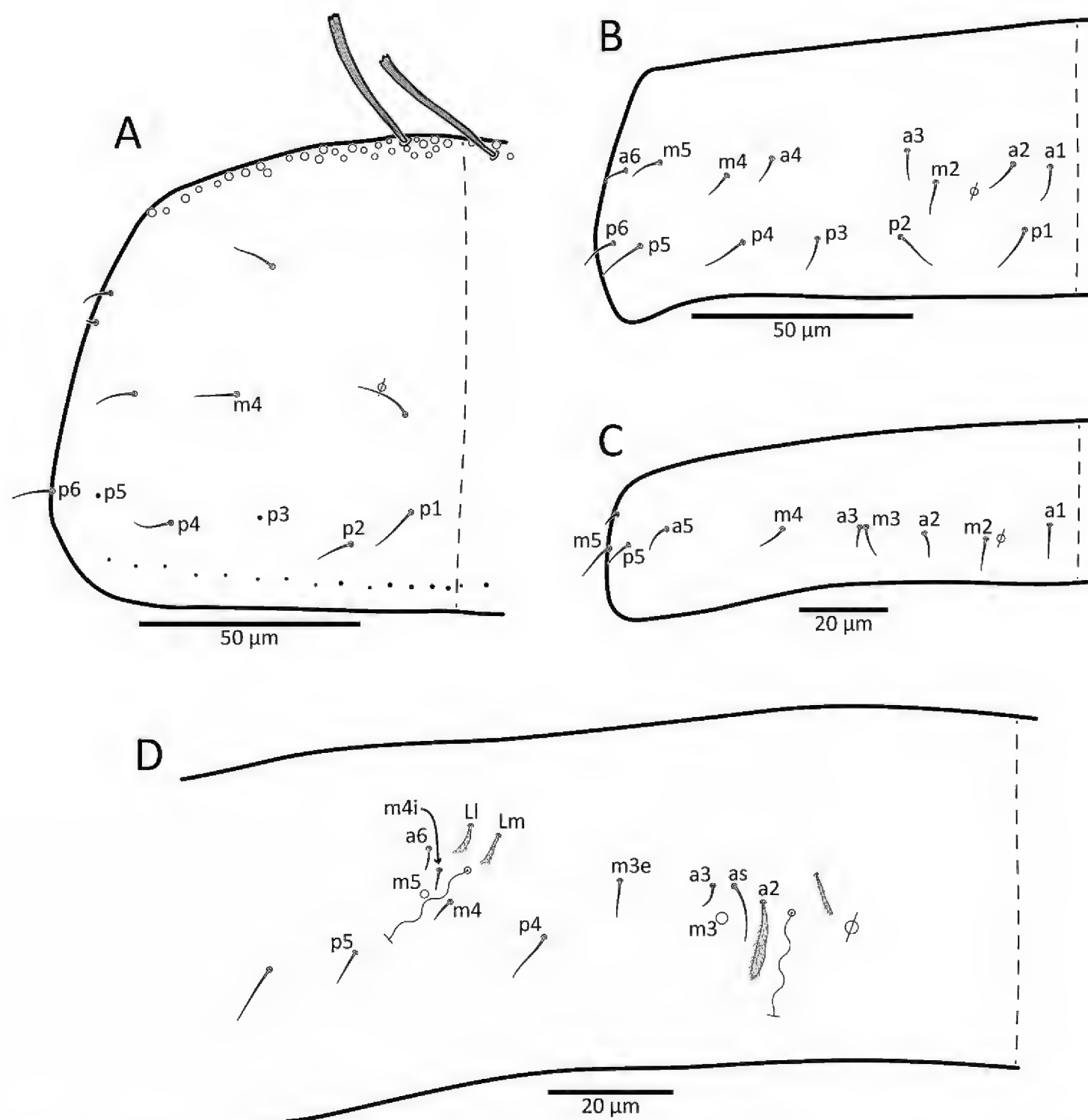


Figure 19. *Pseudosinella vulcana* sp. n. **A–D** dorsal chaetotaxy: **A** Th. II **B** Th. III **C** Abd. I **D** Abd. II.

Legs. Trochanteral organ with up to 9 setae. Metatibiotarsi with 2 outstanding posterior blunt seta. Tenent hair short and acuminate. Unguis with 4 inner teeth; 1 large wing-like inner tooth with 2 basal minute paired lateral teeth, and 1 unpaired proximal tooth. Unguiculus basally swollen on all legs; with 1 large outer wing tooth (Fig. 20C).

Ventral tube. Lateral flaps with 4+4 or 5+5 smooth setae, anterior face with 4+4 ciliate setae, and posterior face (Fig. 20D) with 1+1 smooth setae and 1+1 minute conic microsensilla.

Furcula. Dens tubercle absent. Mucro with sub-apical tooth larger than apical tooth; basal spine smooth.

Remarks. *Pseudosinella vulcana* sp. n. is the only member of the genus with 1+1 eyes and with a wing tooth on both the unguis and unguiculus. This new species is most similar to *P. biunguiculata* Ellis, 1967, *sensu* Mari Mutt (1986), but differs by

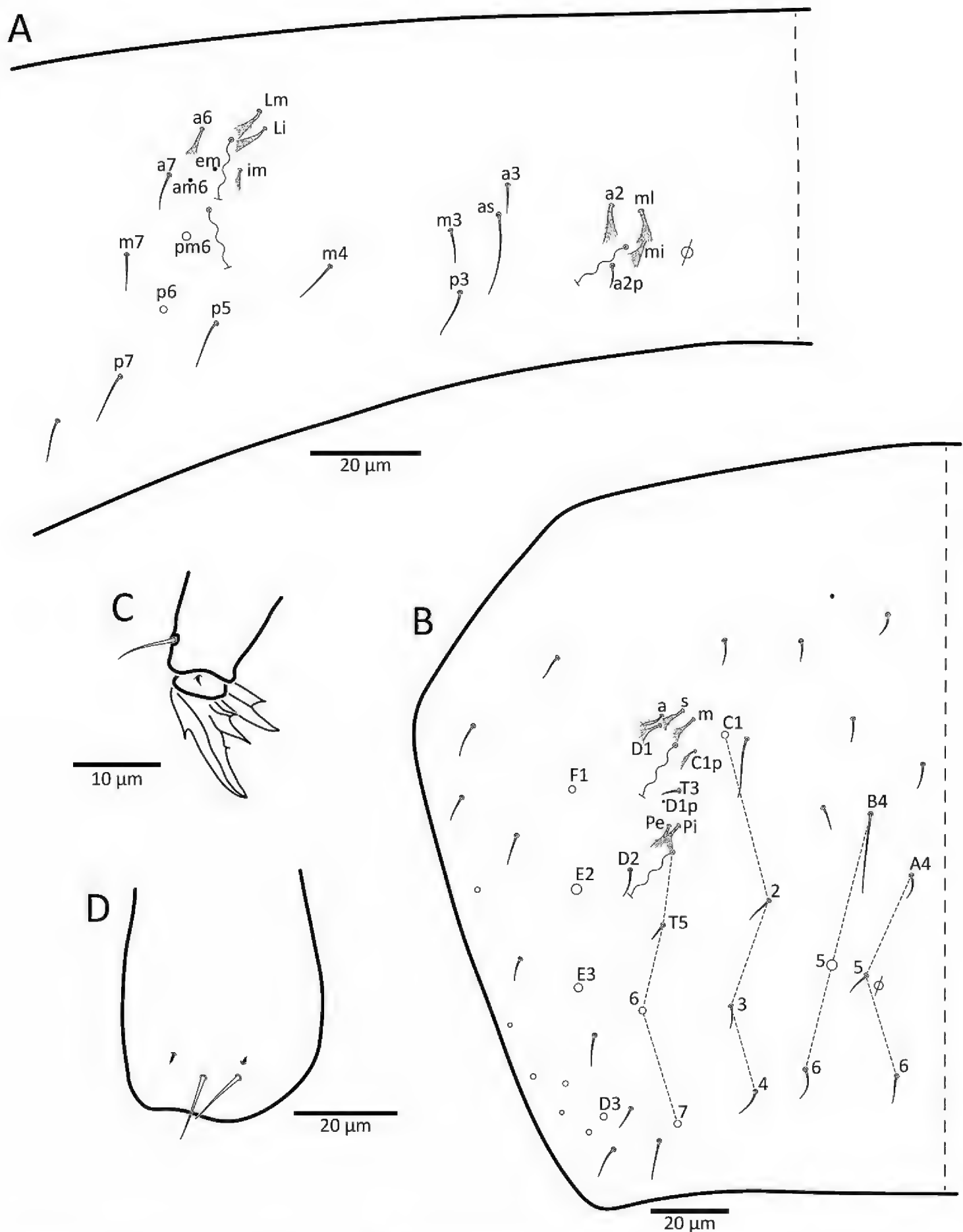


Figure 20. *Pseudosinella vulcana* sp. n. **A–B** dorsal chaetotaxy: **A** Abd. III **B** Abd. IV **C** prothoracic claw complex **D** posterior face of collophore.

having 1+1 eyes, Abd. IV supplemental seta *s* present (Fig. 20B), and only 1+1 paired setae on the posterior face of the collophore (Fig. 20D), where as in *P. biunguiculata* eyes and supplemental seta *s* are absent and the posterior face of the collophore has 2+2 paired setae and 1 unpaired medial seta.

Pseudosinella vulcana sp. n. has 2 thickened, apically blunt metatibiotarsal setae, which was originally thought to differ from *P. biunguiculata* since Mari Mutt (1986) described only 1 blunt metatibiotarsal seta. However, we observed 2 metatibiotarsal setae on *P. biunguiculata* from Puerto Rico (Guajataca Commonwealth Forest, at end of trail #10, leaf litter, 19.v.2009, F. Soto, coll.). *Pseudosinella caoi* Chen, Wang & Christiansen, 2002 and *Pseudosinella fujiokai* Yosii, 1964, *sensu* Christiansen and Belling (1992), also have blunt metatibiotarsal setae, ungual wing teeth, Head Mc A3 (R2), and lack Mc on Th. II and Th. III, but can be differentiated from *Pseudosinella vulcana* sp. n. by characters outlined in Table 2.

Mari Mutt (1986) described 3 morphologically distinct forms among and within populations of *P. biunguiculata* in Puerto Rico that differ in dorsal chaetotaxy (presence/absence of head Mc A3 (R2)) and tenent hair morphology (clavate/acuminate). He also noted differences between the Puerto Rican forms and Ellis' (1967) type specimens; primarily the absence of head Mc A2 (R1), A3 (R2), and Pa5 (Po) on the holotype. Furthermore, the original description of *P. biunguiculata* does not show the presence of m4i on Abd. II, which is distinctly present in the Puerto Rico populations. The high levels of morphological variation exhibited among these forms suggest that *P. biunguiculata* represents a species complex: small and seemingly insignificant differences in morphology have been shown to correlate with large genetic distances among populations, indicating the presence of species complexes (Porco et al. 2012, Cicconardi et al. 2013, Katz et al. 2015a). In fact, Soto-Adames (2002b) observed large genetic differences between sympatric individuals of Puerto Rican *P. biunguiculata*, but these differences could not be correlated with differences in morphology due to destructive DNA extraction methods. Additional investigations utilizing morphological and molecular data may clarify species-level relationships among populations of *P. biunguiculata*, a species with a widespread neotropical distribution. See Table 2 for a list of diagnostic characters separating the different forms and descriptions of *P. biunguiculata*.

Pseudosinella vulcana sp. n. was collected from entrance and from the surface of a drip pool (Fig. 2A) within the dark zone, in generally cool, moist, low light conditions (Table 3), suggesting the species may be a troglophile.

Distribution. Santa Cruz Island, Galápagos, Ecuador.

Coecobrya sp. A

Fig. 21A

Remarks. A single juvenile male with 1+1 eyes was collected on the surface (Table 3) at Cueva Gallardo. Four species of *Coecobrya* with 1+1 eyes have been described (Xu and Zhang 2015): *C. boneti* (Denis, 1948), *C. indonesiensis* (Chen & Deharveng, 1997), *C. sanmingensis* Xu & Zhang, 2015, and *C. tukmeas* Zhang, Deharveng & Chen, 2009. Our specimen is very similar to the four species listed above, but the combination of characters on the labial triangle, Abd. III, and unguiculus suggest our specimen represents an undescribed species. Unfortunately, a single juvenile is insufficient material on

Table 2. Diagnostic characters of *Pseudosinella vulcana* sp. n. in relation to *P. biunguiculata* (4 morphological forms from Puerto Rico with locations(s) indicated in parentheses, and the holotype), *P. fujiiokai*, and *P. caoi*. Present (+), absent (-), not reported (?).

Species/forms	Eyes	Labial triangle seta r	Number of blunt setae on metatibiotarsi	Hd A2 (R1)	Hd A3 (R2)	Hd Pa5 (Po)	Abd. 2 m4	Abd. 2 m4i	Abd. 4 suppl. seta s	Tenent hair	Unpaired unguual tooth
<i>Pseudosinella vulcana</i> sp. n.	1+1	+	2	+	+	+	+	+	+	acuminate	+
<i>P. biunguiculata</i> (Gua'jataca)	0	+	2	+	+	+	+	-	-	acuminate	+
<i>P. biunguiculata</i> (Mayagüez, Caguas)	0	+	1	+	+	+	+	+	-	acuminate	+
<i>P. biunguiculata</i> (Mayagüez, Manatí)	0	+	1	+	-	+	+	+	-	clavate	+
<i>P. biunguiculata</i> (Utuado)	0	+	1	+	-	+	+	+	-	acuminate	+
<i>P. biunguiculata</i> Holotype Ellis, 1967	0	+	1	-	-	-	?	-	-	acuminate	+
<i>P. fujiiokai</i> Yosii, 1964	0	+	2	+	+	?	?	-	?	acuminate	- / +
<i>P. caoi</i> Chen et al., 2002	0	-	2-3 (rarely 4)	+	+	+	-	-	-	acuminate	-

Table 3. Environmental conditions associated with March 2014 collections of Entomobryoidea from lava tube sites on Santa Cruz and Isabela islands, Galápagos Islands, Ecuador.

Species	Light (Lux)	Relative humidity (%)	Air temperature (°C)	Soil temperature (°C)	Elevation (m)	Cave zone
<i>Heteromurus (Heteromurtrella) nitens</i>	-	-	-	-	379	-
<i>Lepidocyrtus nigrosetosus</i>	19–794	75.7–85.6	21.9–27.1	21.3–22.9	275–373	Entrance, Twilight
<i>Pseudosinella stewartpecki</i> sp. n.	-	-	-	-	251	Entrance
<i>Pseudosinella vulcana</i> sp. n.	0–702	75.7–92.3	21.9–25.5	21.3–21.8	373	Entrance, Dark
<i>Coecobrya</i> sp. A	13,260	71.7	28.6	26.7	213	Surface
<i>Entomobrya darwini</i> sp. n.	702–13,260	71.7–75.7	25.5–28.6	21.3–26.7	213–275	Surface, Entrance
<i>Cyphoderus</i> cf. <i>agnostus</i>	-	-	-	-	251	Entrance
<i>Salina</i> sp. A	13,260	71.7	28.6	26.7	275	Surface

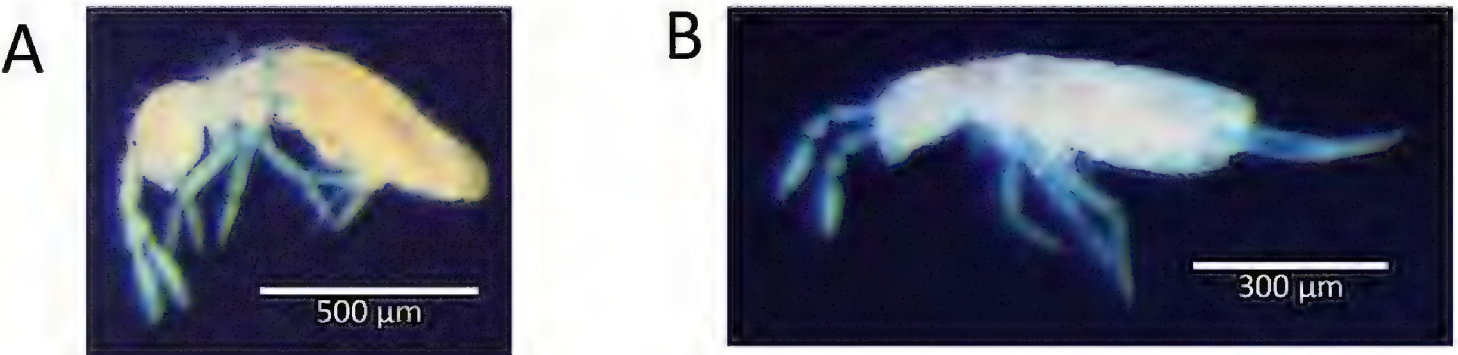


Figure 21. A *Coecobrya* sp. A habitus (INHS Acc. 567,421) **B** *Cyphoderus* cf. *agnostus*, habitus.

which to base a new species description. However, this is the first record of the genus *Coecobrya* from the Galápagos Islands.

Material examined. Ecuador, Galápagos, Santa Cruz Island: 1 juvenile ♂? on slide, Cueva Gallardo, leaf litter near entrance, 8.iii.2014 (S. Taylor and J. Jacoby), GLP-047, INHS Acc. 567,421.

***Entomobrya darwini* Katz, Soto-Adames & Taylor, sp. n.**
<http://zoobank.org/12CC806B-39AD-4F2A-B7E8-3535CE594FDD>
Figs 22–24

Etymology. A patronym honoring the naturalist Charles R. Darwin (1809–1882) for his work on the Galápagos Islands, which helped inspire his contributions to evolutionary theory. We believe Charles Darwin would have overcome his views on Collembola had he seen the color patterns of this new species: “They [Collembola] are wingless, dull-coloured, minute insects with ugly, almost misshapen head and bodies” (Darwin 1871).



Figure 22. *Entomobrya darwini* sp. n. **A** habitus (INHS 567,423) **B–H** dorsal and lateral color pattern variation of four individuals: **B–C** (INHS Acc. 567,422) **D–E** (INHS Acc. 567,425) **F–G** (INHS Acc. 567,424) **H** (deposited at CDRS).

Type material. *Holotype*, ♀ on slide, Ecuador, Galápagos, Santa Cruz Island: Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, INHS Acc. 567,422.

Paratypes, Ecuador, Galápagos, Santa Cruz Island: 1 on slide, Cueva Cascajo, leaf litter from skylight entrance, 9.iii.2014 (S. Taylor, J. Jacoby and M. Sutton), GLP-031, CDRS; 2♂ on slide, Cueva Cascajo, leaf litter from skylight entrance, 9.iii.2014 (S. Taylor, J. Jacoby and M. Sutton), GLP-031, INHS Acc. 567,423 & 567,424; 1♀ on slide, Cueva Gallardo, leaf litter near entrance, 8.iii.2014 (S. Taylor and J. Jacoby), GLP-047, INHS Acc. 567,425; 1♀ on slide, Cueva Chato 2, leaf litter at entrance, 15.iii.2014 (S. Taylor, J. Jacoby, S. Hagan and R. Toomey), GLP-086, INHS Acc. 567,426.

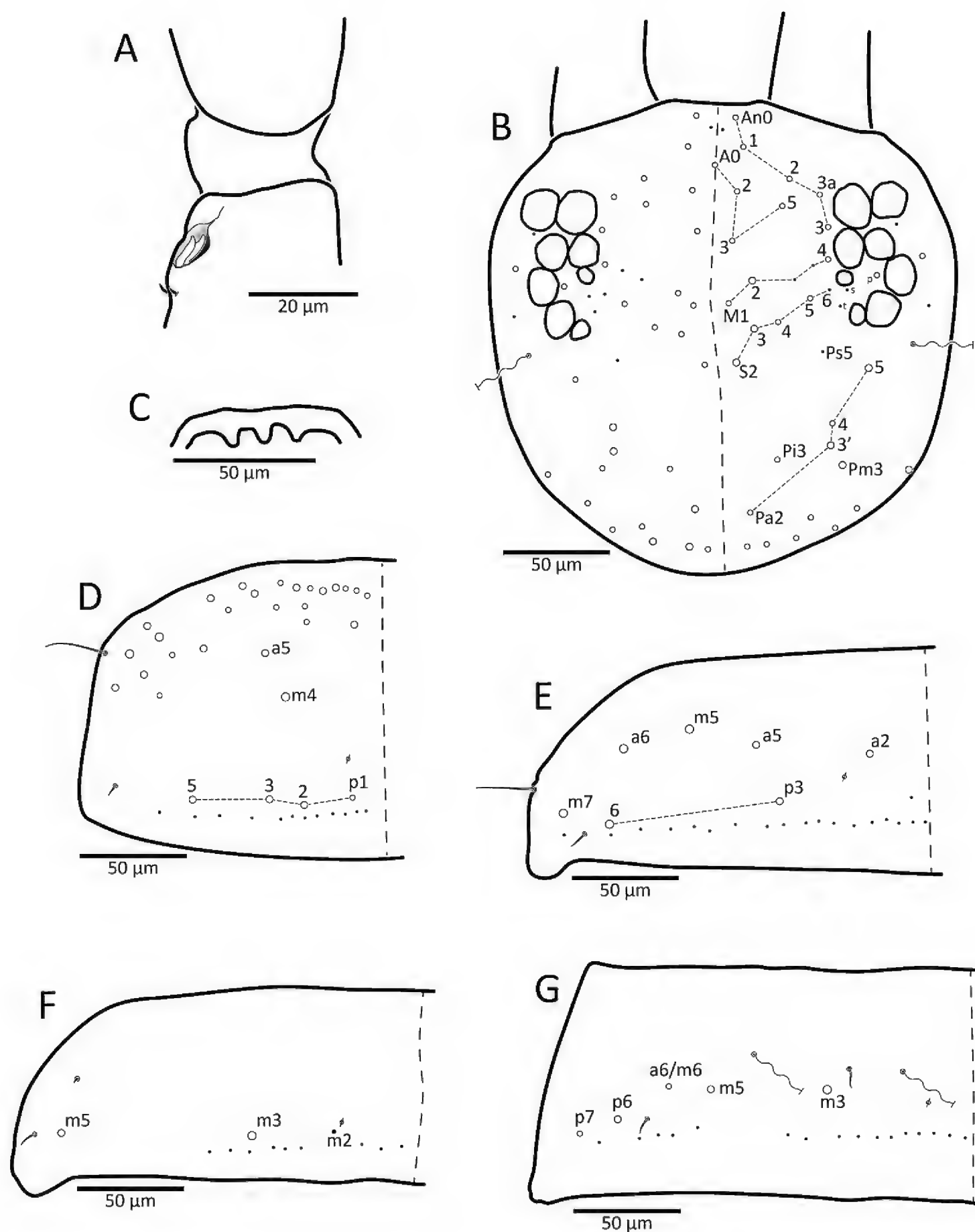


Figure 23. *Entomobrya darwini* sp. n. **A** apical sense organ of Ant. III **B** dorsal chaetotaxy of head **C** labral papillae **D–G** dorsal chaetotaxy: **D** Th. II **E** Th. III **F** Abd. I **G** Abd. II.

Description. *Body shape and color pattern.* Body slightly dorso-ventrally flattened. Length up to 1.57mm (♀) and 1.23mm (♂). Males and females with no obvious difference in color pattern. Color pattern with slight variation (Fig. 22): light orange/tan background with black or dark purple pigment forming two irregular lateral tri-

angles or sometimes broken angled bands on the posterior margin of Abd. III; an additional pair of lateral angled broken bands on Abd. II; dark pigment present along lateral margins of Th. II through Abd. IV, sometimes broken along lateral margin of Abd. III; dark irregular/broken transverse band along posterior margin of Abd. III – Abd. V. Abd. IV usually with an irregular U- or “11”-shaped pattern connecting basally with band along posterior margin. Antennae usually with uniform purple pigment. Legs white, with purple patches on apical end of femora and tibia.

Head. Apical bulb of Ant. IV simple. Apical sense organ of Ant. III enlarged and recessed in shallow pit (Fig. 23A). Apical sense organ on Ant. II with single modified seta. Eyes G and H small and subequal. Eye patch with 3 setae; s, t, and p. Dorsal head chaetotaxy reduced and fixed, no Mc variation observed (Fig. 23B): A6, M3, S'0, S0, S1, S4i, S5i, Ps2, Ps3, and Ps5 always absent; Ps5 present as micro- or mesoseta. Labral setae smooth. Prelabral setae ciliate. Ornamentation of the distal margin of the labral papillae smooth (Fig. 23C). Labial lateral appendage of labial papillae slightly curved, relatively thin, length subequal to apex of labial papilla E. Labial triangle chaetotaxy formula: M1rEL1L2A1-5.

Thorax. Dorsal chaetotaxy of mesothorax reduced and stable, no Mc variation observed (Fig. 23D): a5, m4, and posterior Mc p1, p2, p3, and p5 present; anterolateral sensilla straight and extremely elongated; ms and posterior sensilla present. Dorsal chaetotaxy of metathorax reduced and fixed (Fig. 23E): a2, a5, a6, m5, m7, p3, and p6 present; anterolateral sensilla straight and extremely elongated; additional sensillum observed just internal to P3 in one individual.

Abdomen. Abdominal chaetotaxy reduced and stable; no Mc variation observed. Abd. I with 2 Mc (m3 and m5) present; m₂ present as mesoseta (Fig. 23F). Abd. II with 5 Mc (m3, m5, a6, p6, and p7) (Fig. 23G). Abd. III with 3 Mc (m3, pm6, p6) (Fig. 24A). Abd. IV with 2 inner Mc and up to 11 outer Mc (Fig. 24B). Mucronal sub-apical tooth larger than apical tooth (Fig. 24C).

Legs. Trochanteral organ (Fig. 24D) with up to 9 setae in a triangular pattern; setae thick and apically recurved, increasing in size toward distal margin of trochanter. Unguis (Fig. 24E) with 4 inner teeth: 2 paired basal teeth located approximately middle of inner claw length, and 2 unpaired distal teeth; 3 short, basal outer teeth: 1 dorsal, 2 lateral. Unguiculus lanceolate and serrated. Tenent hair spatulate.

Remarks. *Entomobrya darwini* sp. n. is the only member in this genus with the combination of color pattern and chaetotaxy presented in the description above. In addition, *E. darwini* sp. n. has some unique diagnostic characters that, to our knowledge, have not been previously documented: the conspicuously long lateral sensilla on Th. II and Th. III (Fig. 23D, E) and the spine-like setae on the trochanteral organ are uncharacteristically enlarged, stout, and slightly truncated (Fig. 24D)

This species shares a similar color pattern with *Entomobrya litigiosa fasciata* Denis, 1931 described from Costa Rica, but *E. darwini* sp. n. has two dark broken/irregular triangles or angled bands along the lateral margins of Abd. III that are always absent in *E. litigiosa fasciata*, in addition, the unguiculus is lanceolate in *E. darwini* sp. n., whereas in *E. litigiosa fasciata*, it is truncate. The color forms of the Nearctic species

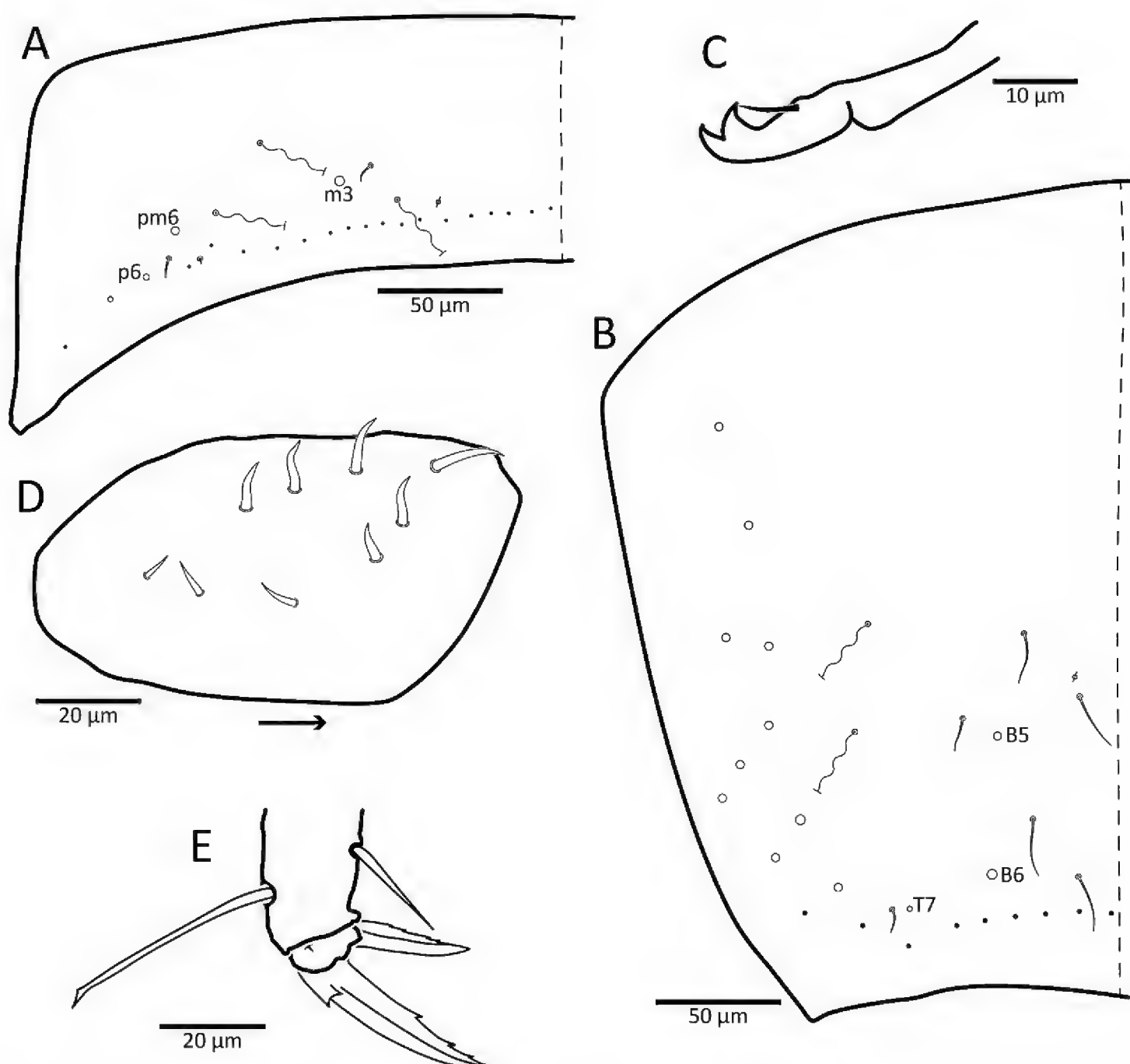


Figure 24. *Entomobrya darwini* sp. n. **A–B** dorsal chaetotaxy: **A** Abd. III **B** Abd. IV **C** mucro **D** trochanteral organ **E** hind claw complex.

Entomobrya decemfasciata (Packard, 1873), *sensu* Katz et al. (2015b), also include angled bands on Abd. III that superficially resemble those exhibited by *E. darwini* sp. n. However, these species can easily be separated by chaetotaxy: *E. decemfasciata* is characterized by having an extreme abundance of dorsal Mc, whereas in *E. darwini* sp. n., the dorsal Mc are generally reduced (Figs 23B, D–G; 24A, B). *Entomobrya nicoleti* (Lubbock, 1871) also shares a similar color pattern with *E. darwini* sp. n. that includes forms with angled lateral bands on Abd. III, but differences in dorsal chaetotaxy (e.g., *E. nicoleti* has a1 on Abd. III that is absent on *E. darwini* sp. n.) easily separates these two species.

Entomobrya darwini sp. n. was collected from both surface and entrance habitats (Table 3) at three caves. This is the first record of the genus *Entomobrya* from the Galápagos Islands.

Distribution. Santa Cruz Island, Galápagos, Ecuador.

Family Paronellidae

Cyphoderus cf. *agnostus* Börner, 1906

Fig. 21B

Remarks. A single individual was collected in the entrance area of a lava tube. Our specimen has a bidentate mucro and the unguis lacks unpaired ungual distal teeth, distinguishing it from *Cyphoderus galapagoensis* Jacquemart 1976 while matching the description of *Cyphoderus agnotus*, *sensu* Cassagnau (1963), albeit Cassagnau's (1963) species description is relatively vague and lacks details about many important characters. Unfortunately, the material available is insufficient for a more complete redescription.

Distribution. Santa Cruz Island, Galápagos, Ecuador; widespread throughout Neotropics.

Material examined. Ecuador, Galápagos, Santa Cruz Island: 1 on slide, La Llegada, leaf litter from entrance, 12.iii.2014 (C. Plowman, D. Butler and G. Hoese), GLP-095, INHS Acc. 567,427.

Salina sp. A Soto-Adames, 2010b

Remarks. A single female, likely a juvenile, was collected. Our specimen keys out to *Salina thibaudi* Soto-Adames, 2010b according to the preliminary key to American *Salina* (Soto-Adames 2010b). However, evaluation of additional characters listed in Soto-Adames (2010b) indicates that this is a new species, similar or identical to *Salina* sp. A from Panama reported in Table 1 in Soto-Adames (2010b). The material available is insufficient to make a complete description and provide an unambiguous diagnosis. Nevertheless, this is the first record of the genus *Salina* from the Galápagos Islands.

This species was collected from a surface habitat adjacent to the entrance of a lava tube (Table 3).

Material examined. Ecuador, Galápagos, Santa Cruz Island: 1♀ on slide, Cueva Cascajo, surface leaf litter near skylight entrance, 9.iii.2014 (S. Taylor, J. Jacoby and M Sutton) GLP-031, INHS Acc. 567,428.

Updated checklist of Superfamily Entomobryoidea (Collembola) of the Galápagos

The following checklist includes all valid entomobryoid species previously reported from the Galápagos Islands, as well as new species records, new genus records, and the three newly described species presented in this paper.

Family Entomobryidae

1. *Coecobrya* sp. A, Santa Cruz Island (new genus record).

2. *Entomobrya darwini* Katz, Soto-Adames and Taylor, sp. n., Santa Cruz Island (new genus record).
3. *Heteromurus* (*Heteromurtrella*) *nitens* Yosii, 1964, Isabela Island (new record).
4. *Lepidocyrtus nigrosetosus* Folsom, 1927, *sensu* Mari Mutt (1986) = *Lepidocyrtus leleupi* Jacquemart, 1976, Santa Cruz Island (Jacquemart 1976; and this report).
5. *Pseudosinella intermixta* (Folsom, 1924), Baltra Island (as South Seymour Island) (Folsom 1924).
6. *Pseudosinella vulcana* Katz, Soto-Adames & Taylor, sp. n., Santa Cruz Island.
7. *Pseudosinella stewartpecki* Katz, Soto-Adames & Taylor, sp. n., Santa Cruz Island.
8. *Seira dowlingi* (Wray, 1953), *sensu* Christiansen and Bellinger (2000) = *Seira caheni* Jacquemart, 1976, Marchena (Peck 2001), San Cristóbal (Peck 2001), and Santa Cruz (Jacquemart 1976) Islands.
9. *Seira galapagoensis* Jacquemart, 1976, Pinzón (Peck 2001), San Cristóbal (Peck 2001), Santa Cruz (Jacquemart 1976), and Santiago (Peck 2001) Islands.

Family Paronellidae

10. *Cyphoderus agnotus* Börner, 1906, Santa Cruz Island (new record).
11. *Cyphoderus galapagoensis* Jacquemart, 1976, Isabela (Peck 2001) and Santa Cruz (Jacquemart 1976) Islands.
12. *Salina* sp. A Soto-Adames, 2010b, Santa Cruz Island (new genus record).

The island records cited above from Peck (2001) were gathered from unknown sources (pers. comm. Peck December 10th, 2015) and need additional confirmation. The following species are listed in Peck and Jacquemart (2013), but are excluded from the checklist above: *Cyphoderus innominatus* Mills, 1938 and *Lepidocyrtus* cf. *lanuginosus* (Gmelin, 1788) do not have formally published records of Galápagos distributions; five additional species names in the genera *Cyphoderus*, *Entomobrya*, *Pseudosinella*, and *Seira* listed in the Charles Darwin Foundation online checklist (Peck and Jacquemart 2013) have not been formally published.

Discussion

Seven species were identified from the collections, including three new species, raising the total number of Galápagos entomobryoids from five to twelve species. Four genera are reported from the Galápagos for the first time: *Coecobrya*, *Entomobrya*, *Heteromurus*, and *Salina*. While none of the entomobryoid species other than *P. vulcana* sp. n. seem to show a particular association with lava tubes, the relatively cool moist conditions found in the entrance and twilight zones of these caves (Fig. 3) provide both a refuge from harsh surface conditions for these and many other organisms, and a window into subsurface volcanic habitats which would otherwise be under-sampled by biologists.

Remarkably, the specimens studied for this paper represent the first new collections of Galápagos Collembola in almost 40 years to be identified and subsequently reported and described. In spite of numerous scientific studies of invertebrates in the Galápagos Island, the new records and new species descriptions presented in this paper and the long gap between new collections being represented in the Galápagos springtail literature suggest that our understanding of the species richness of springtails and other microarthropods in the Galápagos Islands is still incomplete. Additionally, springtail collections from the Galápagos Islands made by Heinrich Schatz (University of Innsbruck) contain dozens of species not presently recorded from the islands (Palacios-Vargas, Pers. Comm. January 2016). Thus, further biological sampling in Galápagos lava tubes and lava tube entrances, sampling of microarthropods from other microhabitats, as well as further taxonomic studies of other material from our 2014 collections, should yield more additions to the fauna of this unique archipelago.

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References

- Addison A (2011) Galápagos — Caving the Equator. *NSS News* 69(6): 8–16.
- Ashmole NP, Oromi P, Ashmole MJ, Martín JL (1992) Primary faunal succession in volcanic terrain: lava and cave studies on the Canary Islands. *Biological journal of the Linnean Society* 46(1-2): 207–234. doi: 10.1111/j.1095-8312.1992.tb00861.x
- Bellinger PF, Christiansen KA, Janssens F (2015) Checklist of the Collembola of the World. Nov. 30, 2015. <http://www.collembola.org> [accessed 15 December 2015]

- Bellini BC, Zeppelini D (2009) Registros da fauna de Collembola (Arthropoda, Hexapoda) no Estado da Paraíba, Brasil. *Revista Brasileira de Entomologia* 53(3): 386–390. doi: 10.1590/S0085-56262009000300012
- Bernard EC, Soto-Adames FN, Wynne JJ (2015) Collembola of Rapa Nui (Easter Island) with descriptions of five endemic cave-restricted species. *Zootaxa* 3949(2): 239–267. doi: 10.11646/zootaxa.3949.2.6
- Börner C (1906) Das System der Collembolen nebst Beschreibung neuer Collembolen des Hamburger Naturhistorischen Museums. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 23: 147–188.
- Bow CS (1979) The geology and petrogenesis of the lavas of Floreana and Santa Cruz Islands, Galápagos Archipelago. Ph.D. Dissertation, Eugene, Oregon, University of Oregon, 308 pp.
- Cassagnau P (1963) Collemboles D'Amérique du Sud. II. Orchesellini, Paronellinae, Cyphoderinae. *Biologie de l'Amérique Australe* 2: 127–148.
- Chen J-X, Christiansen K (1993) The genus *Sinella* with special reference to *Sinella* s.s. (Collembola: Entomobryidae) of China. *Oriental Insects* 27(1): 1–54. doi: 10.1080/00305316.1993.10432236
- Chen J-X, Deharveng L (1997) A new record of the genus *Sinella* in Indonesia with a new species of the subgenus *Coecobrya* (Collembola: Entomobryidae). *The Raffles Bulletin of Zoology* 45(1): 135–138. [http://lkcnhm.nus.edu.sg/nus/pdf/PUBLICATION/Raffles%20Bulletin%20of%20Zoology/Past%20Volumes/RBZ%2045\(1\)/45rbz135-138.pdf](http://lkcnhm.nus.edu.sg/nus/pdf/PUBLICATION/Raffles%20Bulletin%20of%20Zoology/Past%20Volumes/RBZ%2045(1)/45rbz135-138.pdf)
- Chen J-X, Wang F, Christiansen K (2002) A New Species of *Pseudosinella* from Guilin, China (Collembola: Entomobryidae). *Journal of the Kansas Entomological Society* 75(2): 80–85. <http://www.jstor.org/stable/25086048>
- Christiansen K, Bellinger P (1992) *Insects of Hawaii: A Manual of the Insects of the Hawaiian Islands, including an Enumeration of the Species and Notes on their Origin, Distribution, Hosts, Parasites, etc.* Volume 15. Collembola. University of Hawaii Press, Honolulu, 445 pp.
- Christiansen K, Bellinger P (2000) A survey of the genus *Seira* (Hexapoda: Collembola: Entomobryidae) in the Americas. *Caribbean Journal of Science* 36(1–2): 39–75. <http://cro.ots.ac.cr/rdmcnfs/datasets/biblioteca/pdfs/nbina-5669.pdf>
- Christie DM, Duncan RA, McBirney AR, Richards MA, White WM, Harpp KS, Fox CG (1992) Drowned islands downstream from the Galapagos hotspot imply extended speciation times. *Nature* 355: 246–248. doi: 10.1038/355246a0
- Cicconardi F, Fanciulli PP, Emerson BC (2013) Collembola, the biological species concept and the underestimation of global species richness. *Molecular ecology* 22(21): 5382–5396. doi: 10.1111/mec.12472
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle of life.* John Murray, London.
- Darwin C (1871) *The descent of Man, and selection in relation to sex.* Vol. I. John Murray, London. doi: 10.5962/bhl.title.110063
- Denis JR (1931) Contributo alla conoscenza del “microgenton” di Costa Rica. II. Collemboles de Costa Rica avec une contribution au species de l'ordre. *Bollettino del Laboratorio di Zoologia Generale e Agrario, Portici* 23: 69–170.

- Denis JR (1948) Collemboles d'Indochine récoltes de M. C. N. Dawydoff. Notes d'Entomologie Chinoise 12: 183–311.
- Ellis WN (1967) Studies on neotropical Collembola, I. Some Collembola from Guatemala. Beaufortia 14(171): 93–107. <http://www.repository.naturalis.nl/record/504810>
- Folsom JW (1924) Apterygota of the Williams Galapagos expedition. Zoologica 5(5): 67–76.
- Folsom JW (1927) Insects of the subclass Apterygota from Central America and the West Indies. Proceedings of the United States National Museum 72(6): 1–25. doi: 10.5479/si.00963801.72-2702.1
- Folsom JW (1932) Hawaiian Collembola. Proceedings of the Hawaiian Entomological Society 8(1): 51–80.
- Gama MM da (1986) Systématique évolutive des *Xenylla*. XIV. Espèces provenant de Thaïlande, Bornéo, Australie et Norfolk, Galapagos, Mexique et Curaçao (Insecta: Collembola). Revue suisse de Zoologie 93(2): 271–277. doi: 10.5962/bhl.part.79694
- Geist DJ, Harpp KS, Naumann TR, Poland M, Chadwick WW, Hall M, Rader E (2008) The 2005 eruption of Sierra Negra Volcano, Galápagos, Ecuador. Bulletin of Volcanology 70(6): 655–673. doi: 10.1007/s00445-007-0160-3
- Geist DJ, Snell H, Snell H, Goddard C, Kurz MD (2014) A paleogeographic model of the Galápagos Islands and biogeographical and evolutionary implications. In: Harpp KS, Mittelstaedt E, d'Ozouville N, Graham DW (Eds) The Galápagos: A natural laboratory for the earth sciences. John Wiley & Sons, Hoboken, New Jersey, 145–166. doi: 10.1002/9781118852538.ch8
- Gisin H (1967) Espèces nouvelles et lignées évolutives de *Pseudosinella* endogés (Collembola). Memórias e Estudos do Museum Zoológico da Universidade de Coimbra 301: 1–25.
- Global Volcanism Program (2015) Report on Wolf (Ecuador). In: Sennert SK (Ed.) Weekly Volcanic Activity Report, 27 May–2 June 2015. Smithsonian Institution and US Geological Survey. <http://volcano.si.edu/> [accessed 31 December 2015]
- Gmelin JF (1788) In: Linn, Systema naturae, 13th ed., Lipsiae, 1, 2907 pp.
- Gulden B (2015) Worlds longest lava tubes. Jan. 01, 2015. <http://www.caverbob.com/lava.htm> [accessed 16 December 2015]
- Harris AJL, Rowland SK (2015) Chapter 17 – Lava Flows and Rheology. In: Sigurdsson H, Houghton B, McNutt S, Rymer H, Stix J (Eds) The Encyclopedia of Volcanoes (Second Edition). Elsevier Inc., Amsterdam, 321–342. doi: 10.1016/B978-0-12-385938-9.00017-1
- Hernández JJ, Izquierdo I, Oromi P (1992) Contribution to the Vulcanospeleology of the Galapagos Islands. In: Rea GT (Ed.) Sixth International symposium on vulcanospeleology: Hilo, Hawaii August 1991. National Speleological Society, Huntsville, 204–222. http://www.karstportal.org/FileStorage/Intl_Sym_Vul/ISV6BOOK.pdf
- Hey R (1977) Tectonic evolution of the Cocos-Nazca spreading center. Geological Society of America Bulletin 88(12): 1404–1420. doi: 10.1130/0016-7606(1977)88<i:TEOTCS>2.0.CO;2
- Holden JC, Dietz RS (1972) Galápagos Gore, NazCoPac Triple Junction and Carnegie/Cocos ridges. Nature 100: 266–269. doi: 10.1038/235266a0

- Howarth FG (1991) Hawaiian cave faunas: macroevolution on young islands. In: Dudley EC (Ed.) The unity of evolutionary biology, vol 1. Dioscorides Press, Portland, Oregon, 285–295.
- Howarth FG, James SA, McDowell W, Preston DJ, Imada CT (2007) Identification of roots in lava tube caves using molecular techniques: implications for conservation of cave arthropod faunas. *Journal of Insect Conservation* 11(3): 251–261. doi: 10.1007/s10841-006-9040-y
- Husemann M, Habel JC, Namkung S, Hochkirch A, Otte D, Danley PD (2015) Molecular Evidence for an Old World Origin of Galapagos and Caribbean Band-Winged Grasshoppers (Acrididae: Oedipodinae: *Sphingonotus*). *PLoS ONE* 10(2): e0118208. doi: 10.1371/journal.pone.0118208
- Jacquemart S (1976) Collemboles nouveaux des îles Galapagos. Mission zoologique belge aux îles Galapagos et en Ecuador (N. et J. Leleup, 1964-1965) 3: 137–157.
- Jordana R, Baquero E (2005) A proposal of characters for taxonomic identification of *Entomobrya* species (Collembola, Entomobryomorpha), with description of a new species. *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 76(2): 117–134. Available from: <http://hdl.handle.net/10171/27529>
- Juan C, Emerson BC, Oromi P, Hewitt GM (2000) Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology & Evolution* 15(3): 104–109. doi: 10.1016/S0169-5347(99)01776-0
- Juan C, Guzik MT, Jaume D, Cooper SJ (2010) Evolution in caves: Darwin's 'wrecks of ancient life' in the molecular era. *Molecular Ecology* 19(18): 3865–3880. doi: 10.1111/j.1365-294X.2010.04759.x
- Katz AD, Giordano R, Soto-Adames FN (2015a) Operational criteria for cryptic species delimitation when evidence is limited, as exemplified by North American *Entomobrya* (Collembola: Entomobryidae). *Zoological Journal of the Linnean Society* 173(4): 810–840. doi: 10.1111/zoj.12220
- Katz AD, Giordano R, Soto-Adames F (2015b) Taxonomic review and phylogenetic analysis of fifteen North American *Entomobrya* (Collembola, Entomobryidae), including four new species. *ZooKeys* 525: 1–75. doi: 10.3897/zookeys.525.6020
- Lubbock J (1871) Monograph of the Collembola and Thysanura. The Ray Society. J. E. Adlard, Bartholomew Close, London, 265 pp.
- Mari Mutt JA (1986) [1987] Puerto Rican species of *Lepidocyrtus* and *Pseudosinella* (Collembola: Entomobryidae). *Caribbean Journal of Science* 22(1–2): 1–48.
- Mari Mutt JA, Bellinger P (1990) A catalog of the Neotropical Collembola. *Flora & Fauna Handbook* 5, Florida, USA, 237 pp.
- Mills HB (1938) Collembola from Yucatan caves. *Carnegie Institution of Washington* 491: 183–190.
- Najt J, Thibaud J-M, Jacquemart S (1991) Les Collemboles (Insecta) de l'Archipel des Galápagos. I. Poduromorpha. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 61: 149–166.
- Naranjo Morales M, Martín De Abreu S (2015) Fauna subterránea de Gran Canaria, una historia reciente. *Gota a Gota* 9: 1–6.

- Oromí P, Martín JL, Medina AL, Izquierdo I (1991) The evolution of the hypogean fauna in the Canary Islands. In: Dudley EC (Ed.) *The unity of evolutionary biology*, vol 1. Dioscorides Press, Portland, Oregon, 380–395.
- Packard AS (1873) Synopsis of the Thysanura of Essex County, Mass., with Descriptions of a few extralimital forms. *Annual Report of the Trustees of the Peabody Academy of Science* 5: 23–51.
- Peck SB (1990) Eyeless arthropods of the Galapagos Islands, Ecuador: Composition and origin of the cryptozoic fauna of a young, tropical, oceanic archipelago. *Biotropica* 22(4): 366–381. doi: 10.2307/2388554
- Peck SB (2001) *Smaller Orders of Insects of the Galápagos Islands, Ecuador: Evolution, Ecology and Diversity*. NRC Research Press, Ottawa, Ontario, Canada, 278 pp.
- Peck SB, Finston TL (1993) Galapagos islands troglobites: the questions of tropical troglobites, parapatric distributions with eyed-sister-species, and their origin by parapatric speciation. *Memoires de Biospieliologie* 20: 19–37.
- Peck SB, Jacquemart J (2013) CDF Checklist of Galapagos Springtails - FCD Lista de especies de Colémbolos Galápagos. In: Bungartz F, Herrera H, Jaramillo P, Tirado N, Jiménez-Uzcátegui G, Ruiz D, Guézou A, Ziemmeck F (Eds) *Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin*. Charles Darwin Foundation / Fundación Charles Darwin, Puerto Ayora, Galapagos, <http://www.darwinfoundation.org/datazone/checklists/terrestrial-invertebrates/collembola/> [Last updated: 16 Jan 2013]
- Peck SB, Kukalova-Peck J (1986) Preliminary summary of the subterranean fauna of the galapagos islands, Ecuador. Part II. The insects, evolution, and biogeography. *Proc. 9th Intl. Congr. Speleology, Barcelona* 2: 164–169.
- Peck SB, Shear WA (1987a) A new blind cavernicolous *Lygromma* (Araneae, Gnaphosidae) from the Galápagos Islands. *The Canadian Entomologist* 119(2): 105–108. doi: 10.4039/Ent119105-2
- Peck SB, Shear WA (1987b) A new eyeless, stridulating *Theridion* spider from caves in the Galápagos Islands (Araneae, Theridiidae). *The Canadian Entomologist* 119(10): 881–885. doi: 10.4039/Ent119881-10
- Porco D, Bedos A, Greenslade P, Janion C, Skarżyński D, Stevens MI, Jansen van Vuuren B, Deharveng L (2012) Challenging species delimitation in Collembola: cryptic diversity among common springtails unveiled by DNA barcoding. *Invertebrate Systematics* 26(6): 470–477. doi: 10.1071/IS12026
- Reynolds R, Geist DJ, Kurz MD (1995) Physical volcanology and structural development of Sierra Negra, Isabela Island, Galápagos Archipelago. *Geological Society of America Bulletin* 107(12): 1398–1410. doi: 10.1130/0016-7606(1995)107<1398:PVASDO>2.3.CO;2
- Soto-Adames FN (2002a) Four new species and new records of springtails (Hexapoda: Collembola) from the US Virgin Islands and Puerto Rico, with notes on the chaetotaxy of *Metasinella* and *Seira*. *Caribbean Journal of Science* 38(1/2): 77–105.
- Soto-Adames FN (2002b) Molecular phylogeny of the Puerto Rican *Lepidocyrtus* and *Pseudosinella* (Hexapoda: Collembola), a validation of Yoshii's "color pattern species". *Molecular phylogenetics and evolution* 25(1): 27–42. doi: 10.1016/S1055-7903(02)00250-6

- Soto-Adames FN (2008) Postembryonic development of the dorsal chaetotaxy in *Seira dowl- ingi* (Collembola, Entomobryidae); with an analysis of the diagnostic and phylogenetic significance of primary chaetotaxy in *Seira*. Zootaxa 1683: 1–31. <http://www.mapress.com/zootaxa/2008/1/zt01683p031.pdf>
- Soto-Adames FN (2010a) Two new species and descriptive notes for five *Pseudosinella* species (Hexapoda: Collembola: Entomobryidae) from West Virginian (USA) Caves. Zootaxa 2331: 1–34. <http://www.mapress.com/zootaxa/2010/f/zt02331p034.pdf>
- Soto-Adames FN (2010b) Review of the New World species of *Salina* (Collembola: Paronellidae) with bidentate mucro, including a key to all New World members of *Salina*. Zootaxa 2333: 26–40. <http://www.mapress.com/zootaxa/2010/f/zt02333p040.pdf>
- Soto-Adames FN, Anderson E (in press) Two new species and new records of Entomobryoidea (Collembola: Entomobryomorpha) from Nevis, Lesser Antilles. Florida Entomologist.
- Soto-Adames FN, Barra J-A, Christiansen K, Jordana R (2008) Suprageneric Classification of Collembola Entomobryomorpha. Annals of the Entomological Society of America 101: 501–513. doi: 10.1603/0013-8746(2008)101[501:SCOCE]2.0.CO;2
- Stach J (1932) Die Apterygoten aus den Galapagos-Inseln. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebæk. III. Meddelelser fra det zoologiske museum, Oslo 29: 331–346.
- Stone FD, Howarth FG, Hoch H, Asche M (2004) Root communities in lava tubes. In: Culver DC, White WB (Eds) Encyclopedia of caves. Elsevier Academic Press, Burlington, Massachusetts, 477–484.
- Szeptycki A (1979) Chaetotaxy of the Entomobryidae and its phylogenetical significance. Morpho-systematic studies on Collembola (Vol. 4). Państwowe Wydawnictwo Naukowe, Warsaw, 218 pp.
- Taylor SJ, Addison A, Toulkeridis T (2012) Biological potential of under-studied cave fauna of the Galapagos Islands. Revista Geoespacial 8: 13–22.
- Thibaud J-M, Najt J, Jaquemart S (1994) Les Collembolles (Insecta) de l'Archipel des Galapagos. II. Isotomidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 64: 199–204.
- Torres-Carvajal O, Barnes CW, Pozo-Andrade MJ, Tapia W, Nicholls G (2014) Older than the islands: origin and diversification of Galápagos leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*) by multiple colonizations. Journal of Biogeography 41(10): 1883–1894. doi: 10.1111/jbi.12375
- Toulkeridis T (2011) Volcanic Galápagos Volcánico. Universidad San Francisco de Quito, Quito, Ecuador, 360 pp.
- Toulkeridis T, Addison A (Eds) (2015) Abstract volume & field guide, 16th International Symposium of Vulcanospeleology & 2nd Simposio Internacional de Espeleología, Ecuador - Galápagos. Universidad de las Fuerzas Armadas ESPE, Sangolquí, Pichincha, Ecuador, 166 pp.
- White WM, McBirney AR, Duncan RA (1993) Petrology and geochemistry of the Galápagos Islands: portrait of a pathological mantle plume. Journal of Geophysical Research 98(B11): 19533–19563. doi: 10.1029/93JB02018
- Wray DL (1953) Some new species of springtail insects (Collembola). Nature Notes, Occasional Papers 1: 1–7.

- Wynne JJ, Bernard EC, Howarth FG, Sommer S, Soto-Adames FN, Taiti S, Mockford EL, Horrocks M, Pakarati L, Pakarati-Hotus V (2014) Disturbance relicts in a rapidly changing world: The Rapa Nui (Easter Island) factor. *BioScience* 64(8): 711–718. doi: 10.1093/biosci/biu090
- Xu G-L, Zhang F (2015) Two new species of *Coecobrya* (Collembola, Entomobryidae) from China, with an updated key to the Chinese species of the genus. *ZooKeys* 498: 17–28. doi: 10.3897/zookeys.498.9491
- Yosii R (1964) Some Collembola of the Tonga Islands. *Kontyû* 32(1): 9–17. <http://ci.nii.ac.jp/naid/110003497541/>
- Zhang F, Deharveng L, Chen J-X (2009) New species and rediagnosis of *Coecobrya* (Collembola: Entomobryidae), with a key to the species of the genus. *Journal of Natural History* 43(41–42): 2597–2615. doi: 10.1080/00222930903243970